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The seasonal variation of meat and glycogen content of seven populations of oysters *Ostrea edulis* L. and a review of the literature

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ABSTRACT

An account is given of the variation during 1961 of the condition index of seven populations of oysters in England and Wales. The index was below the average for the year during January to April, rose during the spring, and after a brief dip in July, rose again in the autumn. The percentage of glycogen in the dry meat was directly related to the condition index, but the relation was not constant. The glycogen level was higher for a given level of condition in the early part of the year. Spawning did not appear to be the main cause of the loss of glycogen.

Oysters from the River Roach were generally in poorer condition than those from other areas, whereas those from the River Yealm were exceptionally good.

A detailed review is made of the literature on the condition of oysters throughout the world and attention is drawn to the importance of the fat reserves.

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PART I
Seasonal variation in the condition of *Ostrea edulis*

INTRODUCTION

This paper gives an account of the changes in condition and glycogen content of seven populations of *Ostrea edulis* L. in England and Wales during 1961. The interest in oysters as components of the inshore fauna is stimulated by their food value, and the enhanced esteem in which 'fat' or 'well-fished' stock are held has aroused interest in their variation and biochemistry. The literature contains the results of analyses from a number of species of oysters from different parts of the world, and this is discussed with reference to the data reported in this paper. Few observers have studied several populations at the same time.

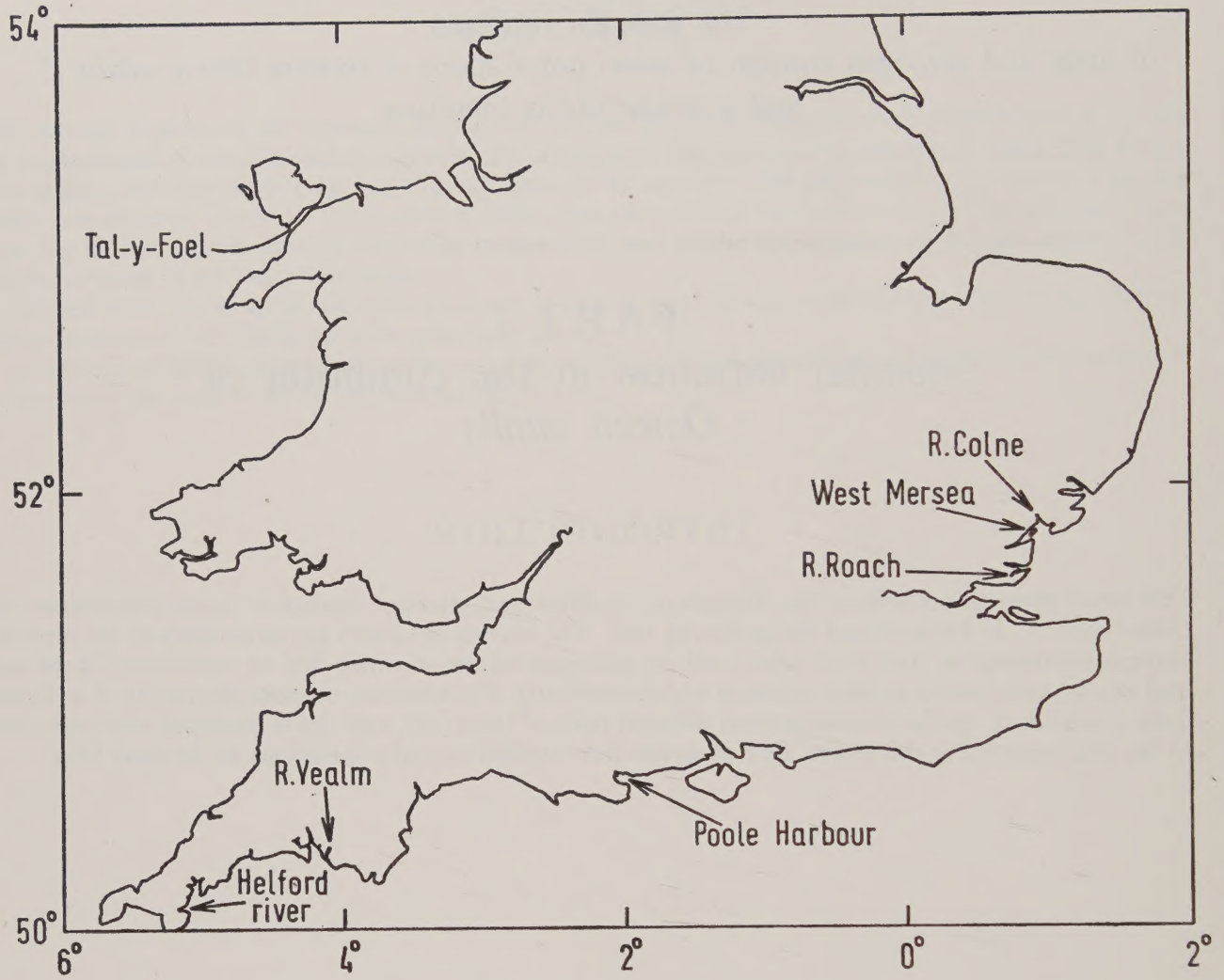


Figure 1 The seven populations of *O. edulis* which were sampled during 1961.

METHOD

Samples of about 60 oysters were obtained, at approximately monthly intervals, from seven populations during 1961 (for position of sampling stations see Figure 1). The samples, with the exception of those from the River Roach and Tal-y-foel, came from commercial sources. Each supplier was asked to send grade 3 oysters from the same stock throughout the year. In practice the size varied considerably between the fisheries, although the average size from any one source was reasonably constant.

The populations examined were as follows:

1. *Helford River, Cornwall* A sheltered estuary which is about five miles long; salinity fluctuations are relatively small. This is one of the largest oyster fisheries in England and recruitment occurs fairly regularly. The stock used were native grown oysters.

2. *River Yealm, Devon* Recruitment rarely occurs in this short estuary, but it has the reputation of producing plump oysters. The stock studied came from the River Fal and had been relaid near Steer Point, where they were subject to considerable salinity variations.

3. *Poole Harbour* This is a large enclosed body of water. The samples were collected from a stock imported from Holland in 1960 and relaid in the South Deep, where only small salinity fluctuations occur.

4. *River Roach* This is an inlet of the sea into which only a small amount of fresh water drains; during the summer salinity is higher than at the other areas examined (Waugh 1957, Mistakidis 1951). The samples collected were native oysters.

5. *West Mersea* The population investigated consisted of Essex oysters relaid in the Strood channel, where the water is shallow and there is little freshwater influence.

6. *River Colne* The samples were collected from oysters, native to the river, which had been relaid in the Pyefleet channel. Here there was little freshwater influence.

7. *Tal-y-foel* This is an experimental fishery and the oysters used had been reared at Conway by the method described by Cole (1938). Temperatures were lower than at most of the other fisheries, but the influence of fresh water is usually small (Walne 1958).

The oysters were sent to Conway by passenger train; the journey did not usually take more than 24 hours, and on arrival they were either examined immediately or placed in running sea water. The latter course was adopted if some of the sample appeared to have lost their shell water. Fifty tightly closed and undamaged oysters were selected at random from the sample. The shells were then cleaned of encrusting epifauna and the oysters weighed in groups of ten. The length (antero-posterior) and breadth (dorso-ventral) of each oyster were measured on a measuring board to the nearest mm below, and the maximum thickness similarly with a caliper gauge.

The condition index was found by successively determining the average whole volume, shell volume, and dry meat weight. The index is then given by the formula:

$$\frac{\text{Dry meat weight (g)}}{\text{Whole volume (ml)} - \text{shell volume (ml)}} \times 1\,000.$$

The use of an index based on the dry weight of meat, instead of the wet meat index used by some workers (Baird 1958, Millar 1961), avoids the very considerable difficulties involved in standardizing the method

of removing and measuring wet meats. Furthermore, the meat can contain variable amounts of water, which can obscure fluctuations in condition (Shaw *et al.* 1967).

The total volume and shell volume were estimated in a displacement jar similar to that illustrated by Baird (1958). Jars large enough to hold 10–50 animals were specially made from tinned steel with an overflow tube fixed near the top. The water displaced by the oysters flowed through this into a graduated cylinder.

After the measurement of the total volume, the oysters were removed from the displacement jar, opened, and the meats extracted and placed in a tared glass jar. Care was taken to ensure that pieces of shell and grit were not included with the meat. When an oyster was found to be brooding, the larvae were washed off the gills and not included in the meat sample. The number of larvae was often estimated, and these data have been used elsewhere (Walne 1964). The shells were blotted dry inside, placed in a displacement jar, and their volume measured. The difference between this measurement and the total volume previously found is the internal volume.

The wet meats were then weighed and the dry weight was estimated as follows: after the meats had been homogenized, three sub-samples of 2 to 3 g were withdrawn, weighed on tared watch-glasses, dried in an oven at 100°C for 24 hours, cooled in a desiccator, and then weighed. This procedure was tested with ten replicate samples which had an average weight of 473 mg after 24 hours' drying. After a further drying period of 24 hours there was an average weight loss of 1.1 mg.

From these data on the percentage of moisture in the homogenized meats of the sample of 50 oysters, the average dry weight per oyster could be calculated. As no attempt was made to standardize the manner in which the meats were drained when they were removed from the shell, no significance can be attached to the water content.

Portions of the homogenized meats were used for the determination of glycogen; 200 ml of homogenate was preserved by the addition of 80 ml of a 10 per cent solution of formaldehyde, and then sent to the Laboratory of the Government Chemist for analysis. Preliminary analyses showed that there was negligible change in the glycogen content of homogenized meats preserved in this manner for several months. The method of analysis used has been described by Fraser *et al.* (1956) and Fraser and Holmes (1958), and with specific reference to oysters by Fraser and Holmes (1961). The principle of the method is to disperse the glycogen in acidified calcium chloride solution after precipitation of the protein, and to measure the amount present in the solution by polarimetry. In some samples a little free glucose was present. This was measured separately and added to that found by polarimetry. The results of the glycogen analysis are therefore the sum of the glycogen and the free glucose, and are expressed as a percentage of the dry meat weight; from this the weight of glycogen per oyster can be calculated and, in turn, a glycogen condition index.

RESULTS

SEASONAL VARIATION

Table 1 gives the three indices of condition which have been determined—dry meat condition index, glycogen condition index, and percentage glycogen—for each sample examined. In some months two results are shown; these are not from duplicate samples but arise when two samples were sent in the same month (usually at the beginning and the end). These data are summarized in the form of cumulative curves in Figure 2. These show that 50 per cent of the population had values above 120 for dry weight condition, 41 for glycogen condition and 34 for percentage glycogen.

In Figure 3 the mean values of these three condition indices for each month are plotted to show their seasonal trend, together with the air temperature. The latter is a mean value calculated from the mean monthly air temperatures (Table 2), for stations near each fishery, as given by the monthly weather record of the Meteorological Office. For most of the fisheries water temperatures are not available, but air temperatures give a useful indication. This is shown by Figure 4 which compares the mean monthly water temperature for Blackpoint in the River Crouch with the air temperature for Southend, seven miles to the south-east. A similar correlation has been given previously for water temperature at Tal-y-foel and the air temperature at Valley (Walne 1958). In general the east coast stations were cooler than the west coast ones in January, February, November and December, and warmer in June, July and August.

There is a considerable range to the confidence limits of the mean values of the indices shown in Figure 3. This is partly due to the substantial disparity in the general level of condition of the oysters in the seven different populations, and this tends to obscure the seasonal trends. This source of variation can be removed by using not the individual indices (**i**) but their difference from the mean ($\bar{\mathbf{i}}$) for the year for that fishery; it is convenient to express this difference as a percentage of the yearly mean and to transform this to $\log_{10}$ to reduce the magnitude of the numbers involved. This transformed index has been calculated for each sample according to the following formula:

$$\log_{10}\left[100\,\frac{\bar{\mathbf{i}}-\mathbf{i}}{\bar{\mathbf{i}}}\right].$$

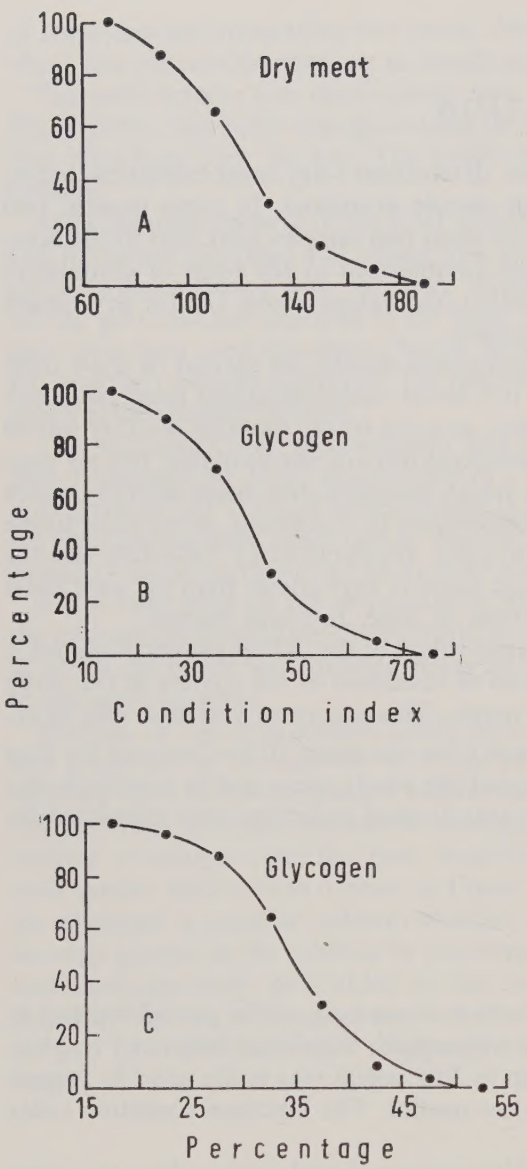
The dry meat condition is plotted on this basis in Figure 5A which shows how, in the period January to April, this index was below average in 22 out of the 25 samples examined. Condition improved in May, and by June the index was well above average; there was a dip in July which was made good in August and September; the late autumn and winter was a period of slow decline. The glycogen condition index (Figure 5B) moved in a similar manner.

The events of the year can be summarized as follows: in the late winter and early spring there was some decline in the glycogen index, but the overall index did not change very much. Between the April and June samples there was a rapid increase in both the glycogen and non-glycogen indices. For the rest of the year the movement of the overall index was largely influenced by variations in the glycogen content. This declined in July, but subsequently recovered and reached its maximum value in September.

The important interrelation between the percentage glycogen and the dry meat condition index is emphasized in Figure 6, where the percentage of glycogen in individual samples is related to the overall dry meat condition index. The samples have been divided into three seasons, as follows:

A January to April, the period before growth begins.
B May to August, which includes the main growth and spawning period.
C September to December, which covers the initial part of the period of winter dormancy.

In each period there was a positive correlation which was significant at the 1 per cent level, but although the relation in the last two periods was similar, in the samples from January to April the percentage of glycogen for a given level of condition was higher. This emphasizes that the non-glycogen fraction has an important influence on condition; at the end of 1961 the oysters contained, on average, about 30 per cent more of this fraction than they did at the beginning of the year.



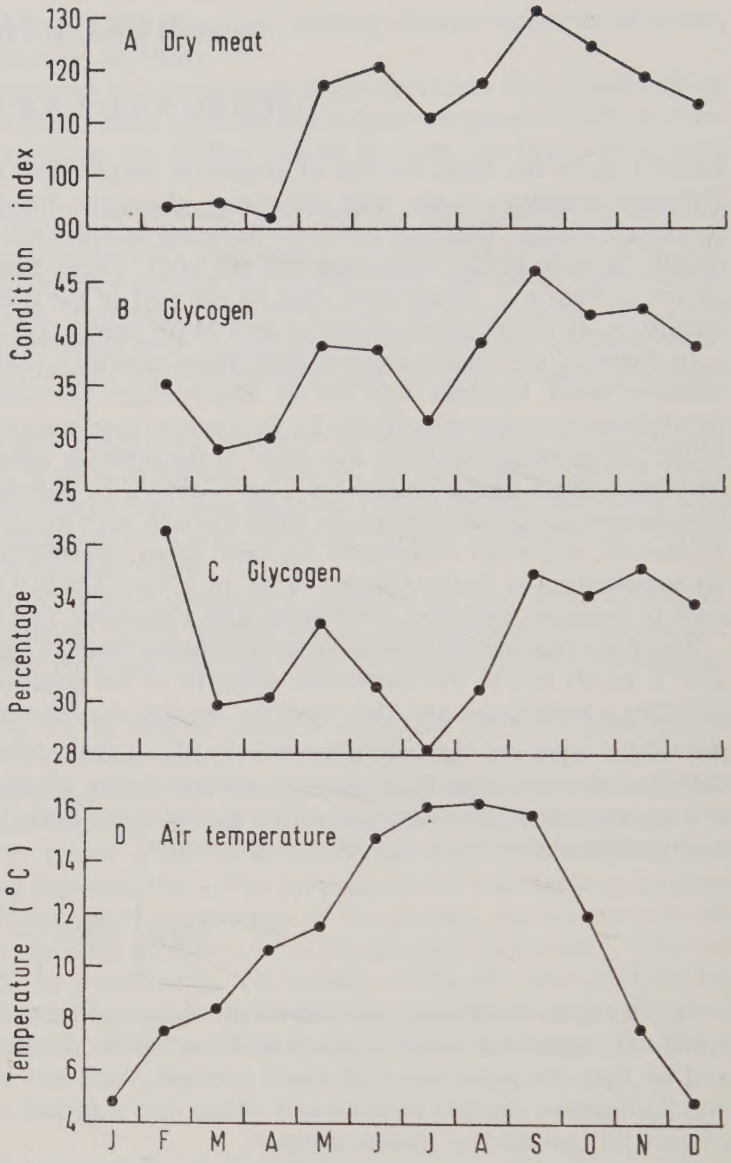


Figure 2 (*left*) Summary of the three indices of condition in *O. edulis*, as cumulative curves showing the proportion (vertical scale) of samples which exceed successive values (horizontal scale).

Figure 3 (*right*) The average monthly values for the three condition factors in *O. edulis*, related to air temperature.

Table 1 The seasonal variation in the condition of oysters in the samples taken in 1961, as shown by A: the dry meat condition index, B: the glycogen condition index, C: the percentage of glycogen in the dry meat. The confidence limits of the mean values are given at the 5 per cent level

1961	Helford River	River Yealm	Poole Harbour	River Roach	West Mersea	River Colne	Tal-y-foel	Mean
A Jan	–	127	69	–	101	–	68	–
Feb	89	130	78	89	–	112	67	94.2±24.2
Mar	81	130	89	94	90, 94	110	71	94.9±15.1
Apr	80	120	110	78	75, 101	104	69	92.1±15.8
May	120, 138	–	128	92	–	118	105	116.8±17.2
Jun	121	168	128	101, 88	115	88	155	120.5±24.6
Jul	99	143	102	–	106	97	121	111.3±18.6
Aug	119	164	–	78	107	–	115, 124	117.8±29.2
Sep	114	156	114	91, 102	143	173	154	130.9±24.7
Oct	95	156	113	96	118	169	–	124.5±32.6
Nov	120	139	103	102	124	–	123	118.5±14.7
Dec	111	148	100	90	120	–	–	113.8±27.6
Mean	107.2 ± 11.6	143.7 ± 10.8	103.1 ± 12.6	91.8 ± 5.2	107.8 ± 11.3	121.4 ± 26.8	106.5 ± 22.5	
B Jan	–	–	–	–	34.9	–	19.8	–
Feb	35.0	64.4	20.3	33.2	–	34.2	25.2	35.4±16.1
Mar	24.4	49.5	24.6	28.1	23.9, 27.9	36.8	17.8	29.1± 8.2
Apr	27.2	47.4	31.7	19.6	30.5, 31.1	31.4	21.9	30.1± 7.0
May	45.6, 49.1	–	39.1	31.3	–	33.5	33.6	38.7± 7.6
Jun	40.6	68.2	39.3	29.9, 15.5	52.4	18.1	42.8	38.4±14.6
Jul	32.7	48.3	24.9	–	36.5	16.0	32.6	31.8±11.4
Aug	44.5	60.5	–	16.5	31.3	–	35.2, 46.3	39.0±15.7
Sep	37.2	68.4	39.2	33.7, 29.3	49.6	54.7	55.4	45.9±11.1
Oct	28.3	57.6	37.6	28.4	39.6	68.3	–	41.9±11.3
Nov	43.6	60.1	34.0	28.2	41.7	–	45.4	42.2±11.4
Dec	35.1	58.7	34.2	31.9	34.0	–	–	38.8±13.9
Mean	36.9 ± 5.0	58.3 ± 5.6	32.5 ± 5.0	27.1 ± 4.0	36.1 ± 5.4	36.6 ± 14.7	34.2 ± 8.0	
C Jan	–	–	–	–	34.6	–	29.4	–
Feb	39.1	49.5	25.9	37.2	–	30.6	36.8	36.5± 8.4
Mar	29.6	38.0	27.6	29.7	26.5, 29.7	33.5	24.6	29.9± 3.5
Apr	34.3	39.6	28.7	24.9	22.7, 30.7	29.8	30.9	30.2± 4.4
May	37.7, 35.6	–	30.5	34.3	–	28.1	31.9	33.0± 3.7
Jun	33.3	40.6	30.6	29.5, 17.6	45.5	20.6	27.3	30.6± 7.8
Jul	33.0	33.8	24.5	–	34.6	16.7	26.6	28.2± 7.3
Aug	37.5	36.9	–	21.5	28.9	–	31.0, 37.2	30.5± 6.5
Sep	32.7	43.9	34.2	37.2, 28.6	34.7	31.7	36.3	34.9± 3.8
Oct	30.2	37.0	33.0	29.5	33.7	40.6	–	34.0± 4.4
Nov	36.6	43.0	32.8	28.0	33.5	–	36.8	35.1± 5.3
Dec	31.7	39.9	34.0	35.4	28.2	–	–	33.8± 5.4
Mean	34.3 ± 1.9	40.2 ± 3.2	30.2 ± 2.4	29.4 ± 3.8	31.9 ± 3.6	29.0 ± 6.2	31.7 ± 3.1	

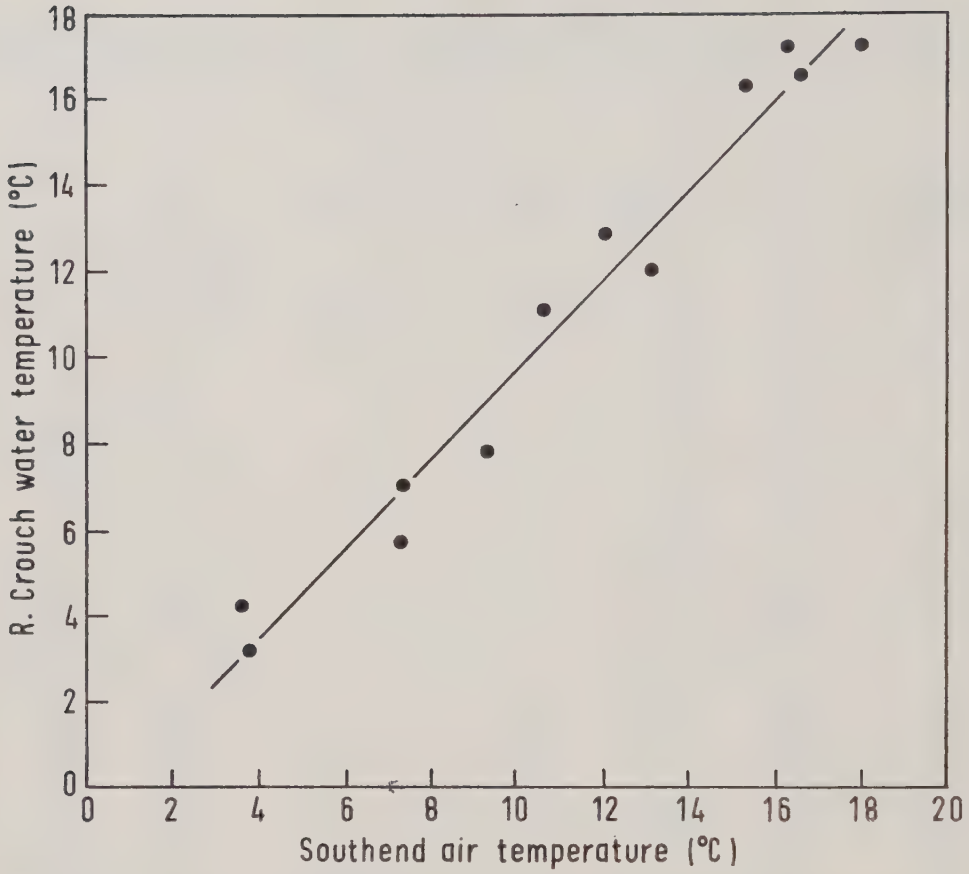


Figure 4 The mean monthly air temperature at Southend in 1961, compared with the mean monthly water temperature at Blackpoint in the River Crouch.

Table 2 The mean monthly air temperature in 1961 from meteorological stations near to the oyster populations examined. (From the Monthly Weather Report of the Meteorological Office)

Oyster population	Nearest weather station	Air temperature (°C)											
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Helford River	Falmouth	6.9	8.9	8.8	–	11.8	14.4	15.8	16.0	14.9	11.7	8.9	7.3
River Yealm	Plymouth Hoe	6.1	8.5	8.5	11.2	11.9	14.3	15.9	16.1	15.7	12.1	8.3	6.5
Poole Harbour	Bournemouth	4.9	7.7	8.0	10.7	11.3	14.5	16.2	16.3	15.9	12.1	7.1	4.3
River Roach	Southend	3.9	7.3	9.3	11.1	12.1	16.3	17.3	17.1	16.5	12.1	7.3	4.3
West Mersea	Maldon	3.7	6.9	7.9	10.3	11.4	15.7	16.5	16.6	16.1	11.1	6.3	3.5
River Colne	Clacton	3.9	6.5	7.9	10.2	11.4	15.5	16.4	16.5	15.9	12.5	7.3	4.1
Tal-y-foel	Valley	5.1	7.4	8.5	9.9	11.1	13.3	14.3	14.9	15.1	11.6	8.1	4.3
Average		4.9	7.6	8.4	10.6	11.6	14.9	16.0	16.2	15.7	11.9	7.6	4.9

The sharp drop in condition in July, which was found in most populations and was associated with a drop in the percentage of glycogen, could be caused by spawning. During this study the number of oysters carrying broods of larvae was recorded and the average percentage of the population found in this condition was as follows: May 0.001, June 6.6, July 10.1, August 2.3. As the samples were taken at monthly intervals and oysters only brood their larvae for 7–10 days, no overlap occurred. Therefore the total proportion of the population which had spawned as female by July was at least 6.6 + 10.1, or 16.7 per cent. If the sexes were equal in number and spawning behaviour, then 16.7 × 2 or 33.4 per cent of the total stock had spawned. This was certainly a minimal number, because many oysters will have spawned in the interval between successive samples.

The decline in condition in July was certainly co-incident with an increase in spawning activity, and some analyses were made to test whether there was a marked decrease in glycogen content in spawning oysters. In July, samples of 200 oysters were obtained from the River Colne and from West Mersea, and 50 of each were set aside for examination in the usual manner. The remainder were opened and condition estimations were made only on those which were found to be brooding larvae (the larvae were discarded). The results (Table 3) show a reduction in the dry meat condition index in breeding females, but little difference in the percentage of glycogen. Indeed, in the Colne sample the breeding females had a substantially higher proportion of glycogen than the whole population.

Later in the year, in respect of a sample from Tal-y-foel, a more rigorous division was made. The last two columns of Table 3 compare the condition and glycogen content of oysters from this population which were brooding larvae and those which were not. Again the loss of condition is clearly seen, but the proportion of glycogen is very similar in breeding and non-breeding animals.

On the basis of this evidence it is unlikely that the generally lower level of glycogen in July was caused by the preferential use of this food reserve during this spawning, since this should show in a more accentuated form in those oysters which were known to have spawned only a few days previously.

Table 3 A comparison between the condition of oysters carrying larvae at the time of examination and that of the whole population. A sample from the River Colne examined on 12 July 1961 gave 18 breeding females and the usual whole population sample contained 6. The sample from West Mersea was examined on 18 July 1961, and here 7 breeding females are compared with the usual population sample which contained 2 breeding females. The Tal-y-foel sample was examined on 12 September 1961 and the results are shown separately for 42 oysters which were not brooding larvae and 15 which were

	River Colne		West Mersea		Tal-y-foel	
	Whole population	Breeding females	Whole population	Breeding females	Non-breeding females	Breeding females
Mean diameter (cm)	7.60	7.91	6.66	6.50	6.61	6.44
Dry meat per oyster (g)	1.52	2.04	1.46	1.36	1.55	1.22
Dry meat condition index	97	74	106	88	154	84
Per cent glycogen	16.7	26.9	34.6	31.2	36.3	34.2
Glycogen condition index	16.0	19.8	36.5	27.3	55.4	28.6

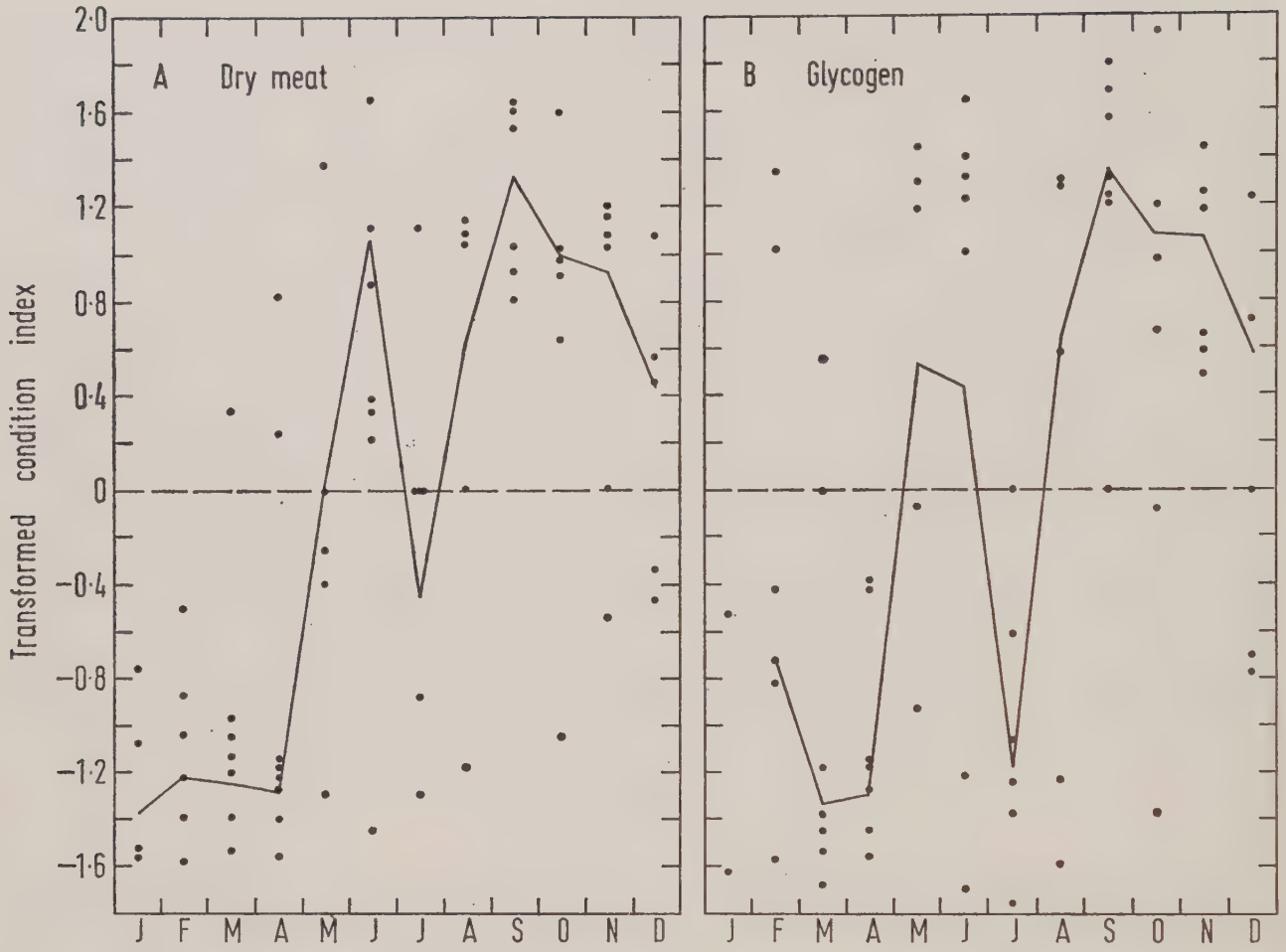


Figure 5 Seasonal variation in A: the dry meat condition index, and B: the glycogen condition index in *O. edulis*. For explanation see text.

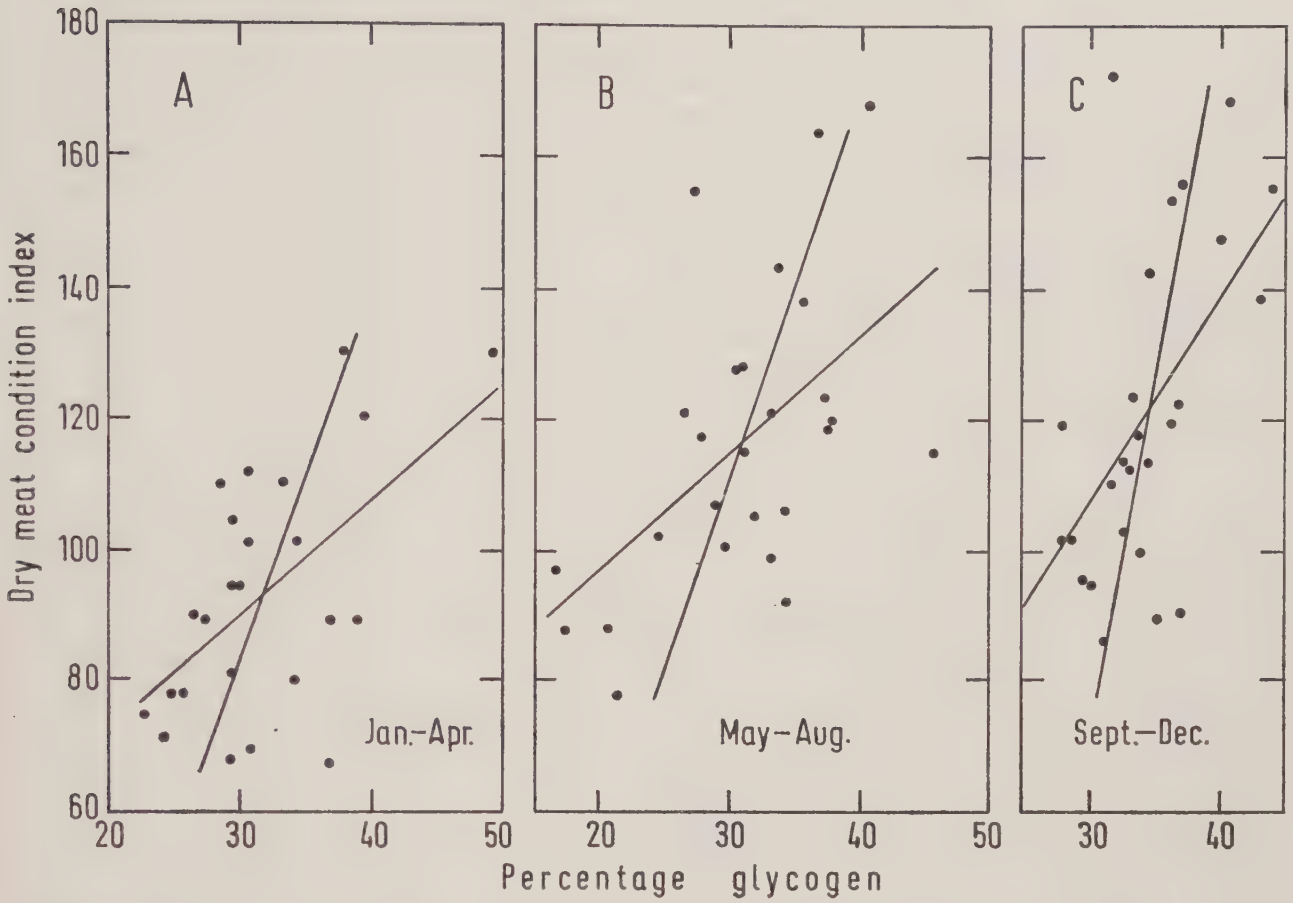


Figure 6 The relation between the dry meat condition index and the percentage of glycogen in *O. edulis*. The calculated regression lines are also shown.

Table 4 The level of the significance of the difference of the various indices of condition in the seven populations of *Ostrea edulis* in 1961. N.S. indicates that the differences were not significant

		Helford River	River Yealm	Poole Harbour	River Roach	West Mersea	River Colne	Tal-y-foel
A	Dry meat condition index	Helford River	1%	N.S.	5%	N.S.	N.S.	N.S.
			River Yealm	5%	1%	1%	N.S.	1%
				Poole Harbour	5%	N.S.	N.S.	N.S.
					River Roach	1%	5%	N.S.
						West Mersea	N.S.	N.S.
							River Colne	N.S.
B	Glycogen condition index	Helford River	1%	N.S.	5%	1%	N.S.	N.S.
			River Yealm	1%	1%	1%	5%	1%
				Poole Harbour	N.S.	5%	N.S.	N.S.
					River Roach	N.S.	N.S.	N.S.
						West Mersea	N.S.	N.S.
							River Colne	N.S.
C	Percentage glycogen	Helford River	1%	N.S.	5%	N.S.	N.S.	N.S.
			River Yealm	1%	1%	5%	5%	1%
				Poole Harbour	N.S.	N.S.	N.S.	N.S.
					River Roach	N.S.	N.S.	5%
						West Mersea	N.S.	N.S.
							River Colne	N.S.

COMPARISON OF POPULATIONS

There were substantial differences in the level of condition (see Table 1) between some of the fisheries, although in most cases the confidence limits of the mean value for the year were fairly high. A more critical examination of the data was made by taking the figures for any two populations and treating the observations for each month as a pair (where more than one observation was made in a month, the mean was used). The significance of the difference between all the pairs of observations for two populations can then be tested, using the standard 't' test procedure. If the differences are statistically different from zero, then this is supporting evidence that the level of condition is higher or lower in one population than in another. This has been done for all possible pairs of populations and Table 4 shows those pairs which were significantly different at the 1 and 5 per cent levels; the direction of the difference can be found by reference to Table 1. Two populations stand out in this analysis: oysters from the River Roach had a significantly lower dry meat condition index than any other population, except for Tal-y-foel, while those from the Yealm were significantly better than any other population, except for the River Colne, for which they were only slightly better.

The glycogen index shows a similar picture, although the Roach sample was not so markedly poor. The Yealm samples had a significantly greater glycogen content than any of the other populations examined. When the percentage glycogen is considered it is seen that the River Yealm oysters were superior to all the other populations, but the Roach sample was only poorer than the Helford, Tal-y-foel and the Yealm. It should be stressed at this point that these differences only apply to condition during one year, and that they tell us nothing about how well the oysters had grown.

It is impossible to do more than speculate on the reasons for the very good values for the oysters from the River Yealm and the rather poor results for those from the River Roach, since virtually nothing is known about the feeding conditions and growth in the various areas at that time. Two possible factors may, however, be of importance; the first refers to the populations, and the second to the hydrographical peculiarities of the areas. The average sizes of the oysters in the samples obtained from a population were similar throughout the period of investigation, but there were substantial differences between the populations. Figure 7 illustrates this and also shows how the ratio of the shell volume to the total volume differed in some cases between populations. Oysters from the Roach, Poole Harbour and the Yealm were the largest studied, but as these included those populations which were both the best and the poorest in condition, size alone cannot be the important factor. Oysters from the Yealm had a slightly smaller shell volume—and hence larger cavity volume—than those from the other two sources.

The populations were, of course, of different genetical origins (see page 15), and it may be that those in the Yealm were from a particularly good strain. I do not, however, think that this is likely, because in the course of time many different populations of oysters have been laid in this river (spatfall rarely occurs) and it has a commercial reputation for producing oysters of high quality.

The most notable hydrographical peculiarity affecting the Yealm is that this population was probably subjected to greater salinity variation than any of the other populations, because of its position relatively high up the estuary. Conversely, the Roach will have experienced rather high salinities during the summer. The importance of fresh water in bringing nutrients into estuaries has often been stressed (e.g. Nelson 1947) and this may have led to good feeding conditions in the Yealm.

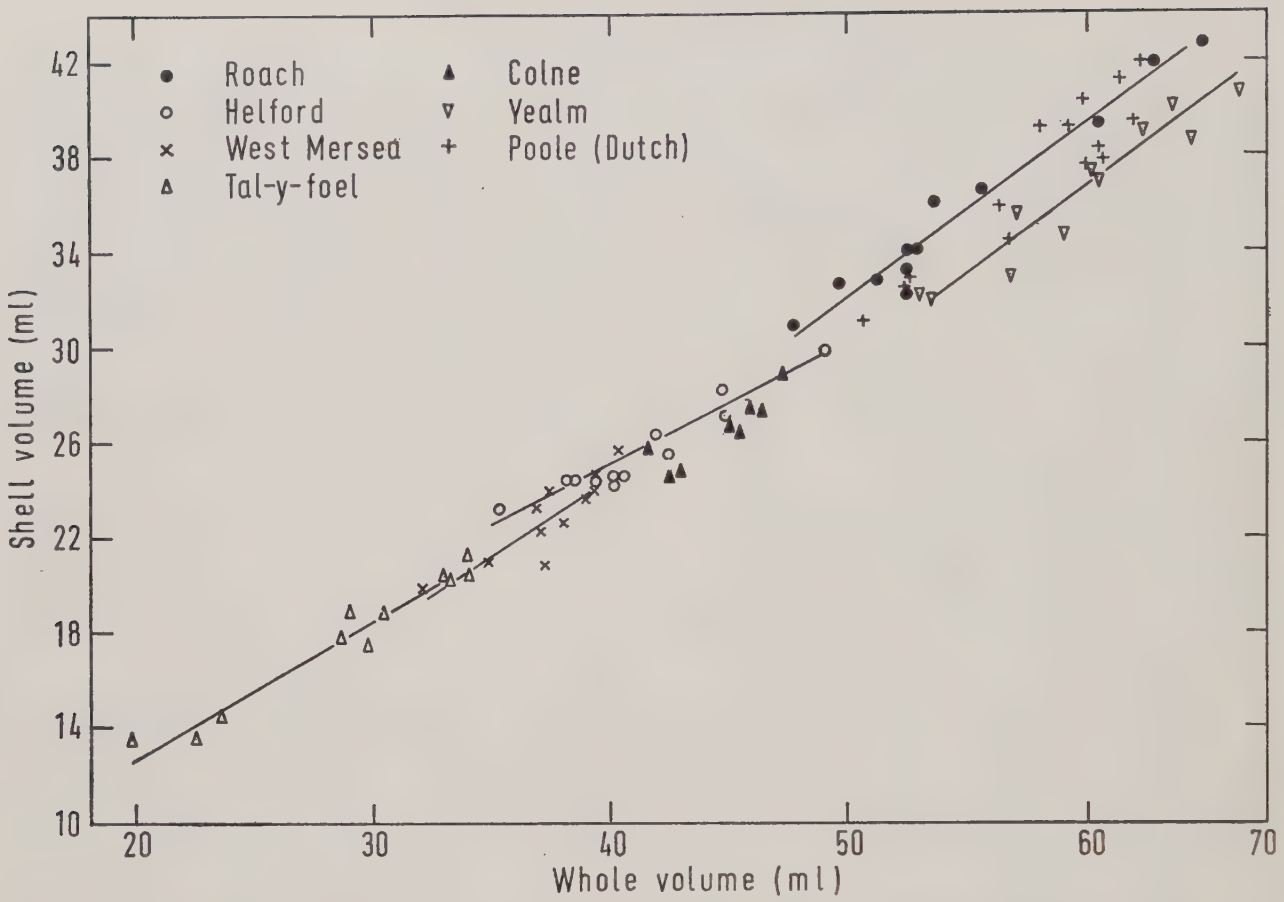


Figure 7 The relation between the mean volume per animal and the mean shell volume per animal in each sample of *O. edulis*.

PART II
Review of published data

INTRODUCTION

The following section reviews the literature which gives quantitative analyses of the condition of various species of oysters from different parts of the world. This task is made more difficult because investigators have measured different parameters and it is not possible to relate all the data to a common basis, for example, internal volume or dry meat weight. The commonest measurement has been the estimation of glycogen (or carbohydrate), expressed as a percentage of the dry or wet meat weight. In some cases this has been linked with a more detailed analysis from which the glycogen content can be related to the total protein. Few authors have attempted to measure condition in the sense of relating meat volume or weight to the space available for it to fill.

Although a number of papers (including the present one) give information on seasonal variation in condition, nowhere is this linked with consideration of the oyster as a growing animal; it has been usual either to examine from time to time a sample of a particular size of animal (as in this paper), or to take a sample that is intended to represent a whole population, without taking adequate precautions to ensure that the sample has a true random composition.

The estimation of the components of the meat as a percentage of the dry weight leads to the difficulty that as one part increases, another must decrease, although in reality what may really be happening is that one constituent is increasing at a faster rate than the other. Where complete analyses have been made this difficulty can be partly overcome by expressing the other components as a percentage of the protein content.

The systematics of the family Ostreidae are, especially in the older literature, in some confusion, but it can be assumed that the oysters discussed are drawn from two genera: *Crassostrea* and *Ostrea*. The most important differences between these two genera are that *Crassostrea* is oviparous and *Ostrea* larviparous, and that ecologically *Crassostrea* tends to occupy the more muddy and estuarine habitats, whereas *Ostrea* is found in the more saline and less silt-laden waters. In the older literature there is sometimes confusion between the two genera.

SUMMARY OF THE LITERATURE

The following papers, listed under the species of oyster examined, have been found to contain information obtained from a number of samples.

Crassostrea virginica The paper by Mitchell (1917) is a pioneer study of condition, but unfortunately only a few samples were examined (the species is not stated, but was presumably *C. virginica*). Medcof (1946) examined the dry meat condition index, at monthly intervals from May to November, of two populations in the Bideford River on Prince Edward Island. Galtsoff *et al.* (1947) present a series of monthly analyses of glycogen, expressed as a percentage of the wet weight, from November 1935 to April 1937, for populations from two branches of Chesapeake Bay—the York and Piankatank Rivers. The water content of the meat is also given and from these data I have calculated the glycogen as a percentage of the dry weight for stations 9 and 20 at the top and bottom of the York River estuary respectively, and for station 55 near the mouth of the Piankatank River. Menzel and Hopkins (1952) give the results of an extensive survey of wet and dry condition factor indices and percentage glycogen for two populations in Louisiana; one was established close to an oil field and the other served as a control. The data from the control population have been used in this paper. Lee *et al.* (1960) examined 51 samples over a 12-month period from shucking houses in the southern states of the U.S.A. The meats were analysed for protein, fat, carbohydrate and ash, but the data are presented in the paper as monthly averages. (An earlier paper, Lee and Pepper 1956, contains few tabulated data). Sakuda (1966) determined the dry weight condition index in samples collected during a year, at two-week intervals, from eight beds in West Loch, Hawaii. Haven (1962) estimated the dry weight condition index from monthly samples of four populations in two branches of the lower Chesapeake Bay during four years.

Crassostrea gigas This species has been examined in detail in Japan. Sekine *et al.* (1929) analysed samples at monthly intervals from Kanazawa. The species investigated is not stated but presumably it was *C. gigas*. Masumoto *et al.* (1934) kept two populations in two places in Hiroshima Bay and samples were analysed in detail at monthly intervals. The results for male and female oysters were recorded separately. Most of the results are given as mean weight per oyster and from this the percentage composition has been calculated. Hatanaka (1940) analysed the composition of nine samples during the late summer and early winter. In a further four samples different tissues were analysed separately. Ogasawara *et al.* (1962) give the results of examining the condition of a considerable number of monthly samples in the period June to December. The samples comprised young oysters from several areas as well as populations which had been transplanted.

C. gigas is imported into North America in large quantities for relaying on to the west coast. Tully (1936) made a detailed analysis of seven samples, collected at intervals over a year, from one plot in British Columbia. Westley (1959, 1960, 1961, 1962, 1963, 1967*a*, *b*) has determined the dry meat condition index of 1 217 samples collected from a number of populations in the State of Washington over the years 1954 to 1965. In his 1959 paper he grades the various levels of condition as follows:

Below 60	Poor	80–100	Good
60–80	Fair	Above 100	Excellent

Crassostrea angulata This species was the subject of a detailed analysis by Graca *et al.* (1956) who examined 26 samples, which were mostly collected from the River Tejo, Portugal, but condition was not determined. Dantec and Raimbault (1965) show the dry meat condition index of populations relaid either in the Bassin d'Arcachon or in two ponds on the Mediterranean coast. Establier (1966) made detailed analyses of 28 samples collected at fortnightly intervals from Cadiz Bay.

Crassostrea commercialis Humphrey (1941) estimated glycogen as a percentage of the wet weight in monthly samples from a station on the Georges River, Australia, and also in a series of 41 miscellaneous samples from the same area. His paper also presents a detailed analysis of 24 samples collected during August from various parts of the Georges River. In recalculating the results for the present paper, four sets of data have been omitted, three because of an unusually low percentage of nitrogen, and the other because the percentage of water and percentage of fat are given as the same.

Crassostrea gryphoides Durve (1964) and Durve and Bal (1961) examined the seasonal variation in condition and in chemical composition in oysters collected 50 miles north-west of Bombay. Venkataraman and Chari (1951) present a full analysis of 29 samples collected at fortnightly intervals from a population near Ennore. They refer to the species as *Ostrea virginiana* Hornell, but it is clear from Hornell's description (Hornell 1916, 1917) that this is a species of *Crassostrea*. In the absence of further information on the systematics, I have considered these studies of Indian oysters as both referring to *C. gryphoides*.

Ostrea edulis Russell (1923) made one of the earliest series of observations when he had 46 samples analysed for fat, protein and glycogen. They were collected, mostly at monthly intervals, from West Mersea, Whitstable, Burnham and Ipswich—all grounds in the vicinity of the Thames estuary. Gaarder and Alvsaker (1941) present the results of monthly samples from two Norwegian polls for 18 months, which included the 1936 reproductive period; unfortunately this proved to be a poor season for growth. I have used the results from the Ytrepoll where the food shortage was less acute. Krvaric (1953) analysed in detail samples of 50–60 oysters, 2–2½ years old, at monthly intervals from the Mali Stou Bay beds in Yugoslavia for a year. Millar (1961) presents the wet meat condition index of layings at 24 sites on the west coast of Scotland, but the oysters were examined individually and the results are given as the percentage of the sample in various condition index groups. This method of presenting the data has not been used elsewhere, and cannot, therefore, be readily used for comparative purposes.

Drinkwaard (1960 and 1961) measured the dry meat condition index in about 50 samples which were collected from the Dutch oyster grounds in the Oosterschelde in June to December in 1958 and 1959. Some data from the same fishery had been presented earlier (Korringa 1956, 1957, 1958, and Drinkwaard 1959), but they are mostly in map form and difficult to extract. It is of interest to note that in one paper Korringa (1956) classifies the various levels of dry meat condition index, according to their commercial acceptability in Holland, as follows:

70	Very poor oyster	100	Good quality oyster
80	Lean	110	Very good oyster
90	Reasonably good	120	Exceptional

Ostrea lutaria Malcolm (1929) examined the chemical composition of a series of seven monthly samples collected during the winter months from the Fouveaux Strait, New Zealand.

Ostrea lurida Tully (1936) made detailed analyses of seven samples collected over a period of a year from one laying in British Columbia. Westley (1959, 1960, 1961, 1962, 1963) determined the dry meat condition index of 323 samples collected from four populations in the State of Washington over the period 1956–1962.

Ostrea circumpicta Okazaki and Kobayashi (1929) estimated the percentage glycogen in the whole body and in the adductor muscle in monthly samples gathered from Mutsu Bay. Unfortunately only four or five animals were examined in each sample.

Table 5 The distribution of dry meat condition index and percentage of glycogen in various oyster populations. For each factor the three columns show the value which was exceeded by 75, 50 and 25 per cent respectively of the samples drawn from each population

Species	Author	Dry meat condition index			Percentage glycogen		
		1st quartile	Median	3rd quartile	1st quartile	Median	3rd quartile
Crassostrea virginica	Medcof 1946	111	123	131	–	–	–
	Galtsoff *et al.* 1947	–	–	–	12	17	24
	Menzel and Hopkins 1952	57	64	71	14	18	24
	Sakuda 1966	63	76	88	–	–	–
	Haven 1962	78	90	103	–	–	–
	Lee *et al.* 1960	–	–	–	24	29	33
Crassostrea gryphoides	Durve and Bal 1961	–	–	–	24	30	32
	Venkataraman and Chari 1951	–	–	–	10	15	19
Crassostrea gigas	Masumoto *et al.* 1934	–	–	–	9	13	18
	Hatanaka 1940	–	–	–	8	13	15
	Westley 1959, 1963, 1967a and b	85	104	125	–	–	–
	Ogasawara *et al.* 1962	63	76	91	–	–	–
Crassostrea angulata	Graca *et al.* 1956	–	–	–	21	24	28
	Establier 1966	–	–	–	16	19	22
	Dantec and Raimbault 1965 (Arcachon)	56	66	76	–	–	–
	Dantec and Raimbault 1965 (Etang)	63	82	95	–	–	–
Ostrea edulis	Russell 1923	–	–	–	30	33	35
	Krvaric 1953	–	–	–	19	22	25
	Gaarder and Alvsaker 1941	–	–	–	31	34	36
	Drinkwaard 1960, 1961	88	102	113	–	–	–
	Walne, this paper	102	120	134	28	34	39
Ostrea lutaria	Malcolm 1929	–	–	–	24	26	28
Ostrea lurida	Westley 1959–1963	85	103	123	–	–	–

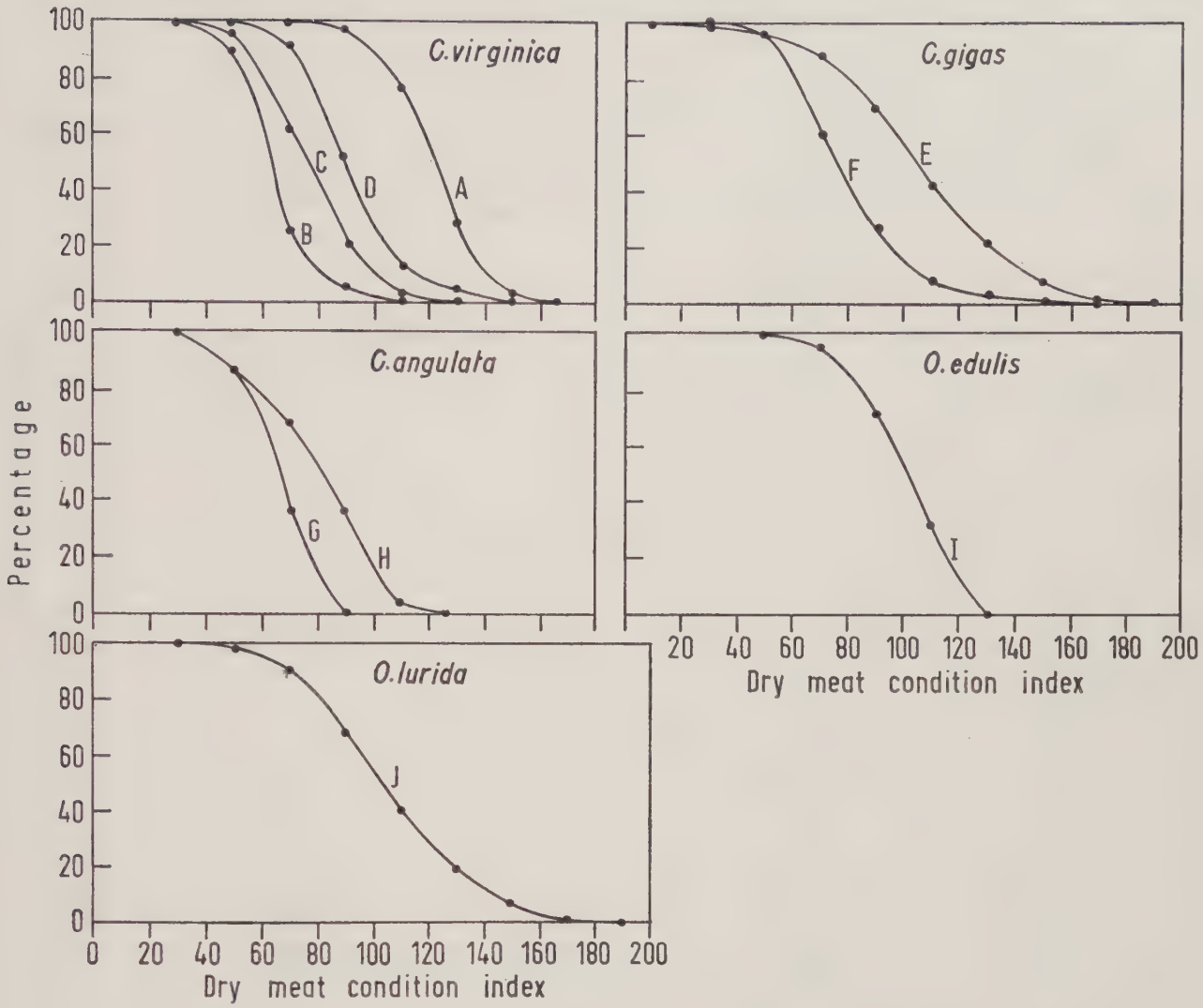


Figure 8 Cumulative curves showing the proportion (vertical scale) of samples which exceeded successive values of dry weight condition index. The origin of the data and the species concerned are as follows: *C. virginica*—A Medcof (1946), B Menzel and Hopkins (1952), C Sakuda (1966), D Haven (1962); *C. gigas*—E Westley (1959 to 1963, 1967a and b), F Ogasawara *et al.* (1962); *C. angulata*—G Dantec and Raimbault (1965, Samples from Arcachon), H Dantec and Raimbault (1965, Samples from Mediterranean 'etang'); *O. edulis*—I Drinkwaard (1960, 1961); *O. lurida*—J Westley (1959 to 1963).

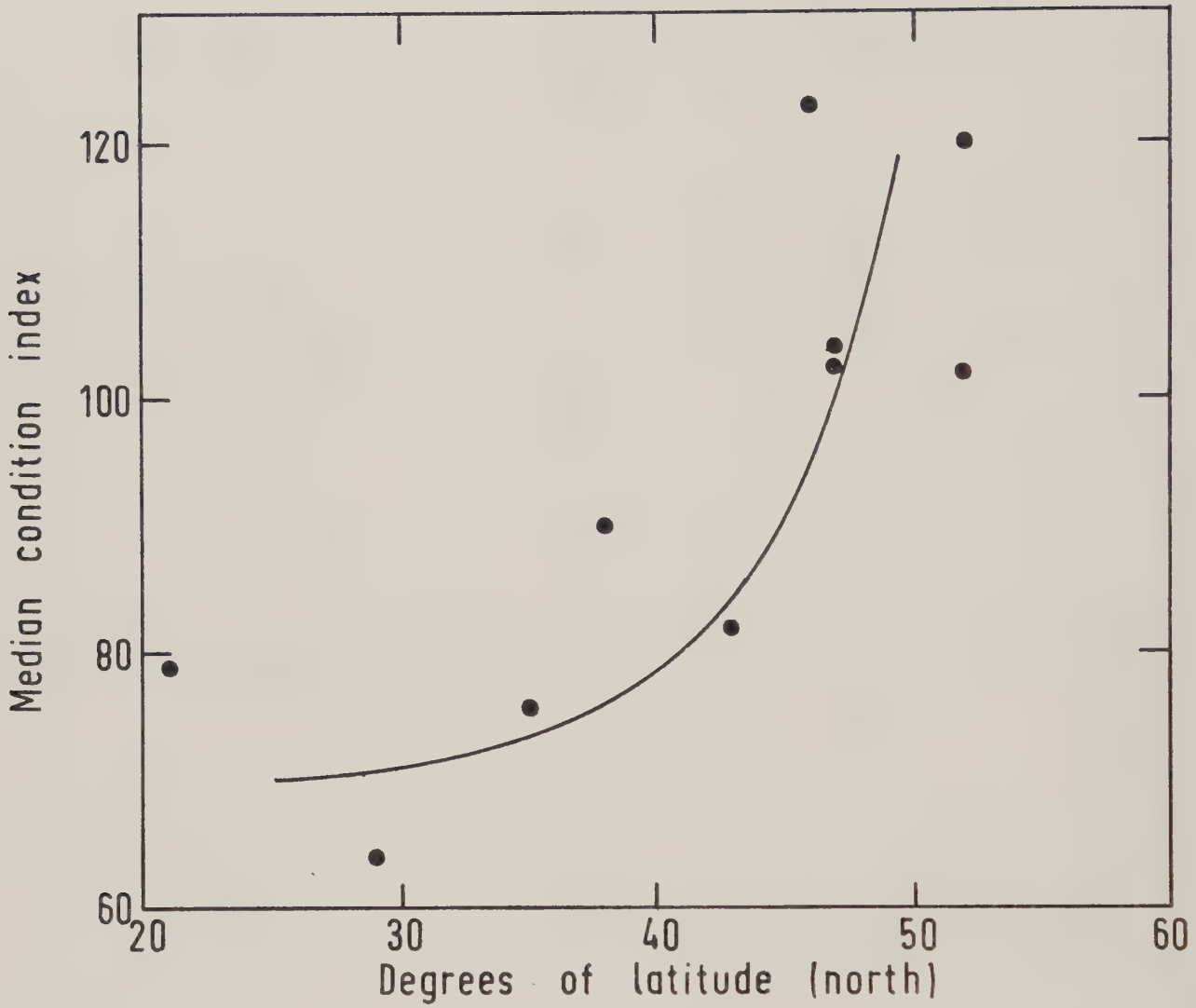


Figure 9 The relation between the values of the median dry meat condition index, as listed in Table 7, and the latitude of the area where the population occurred.

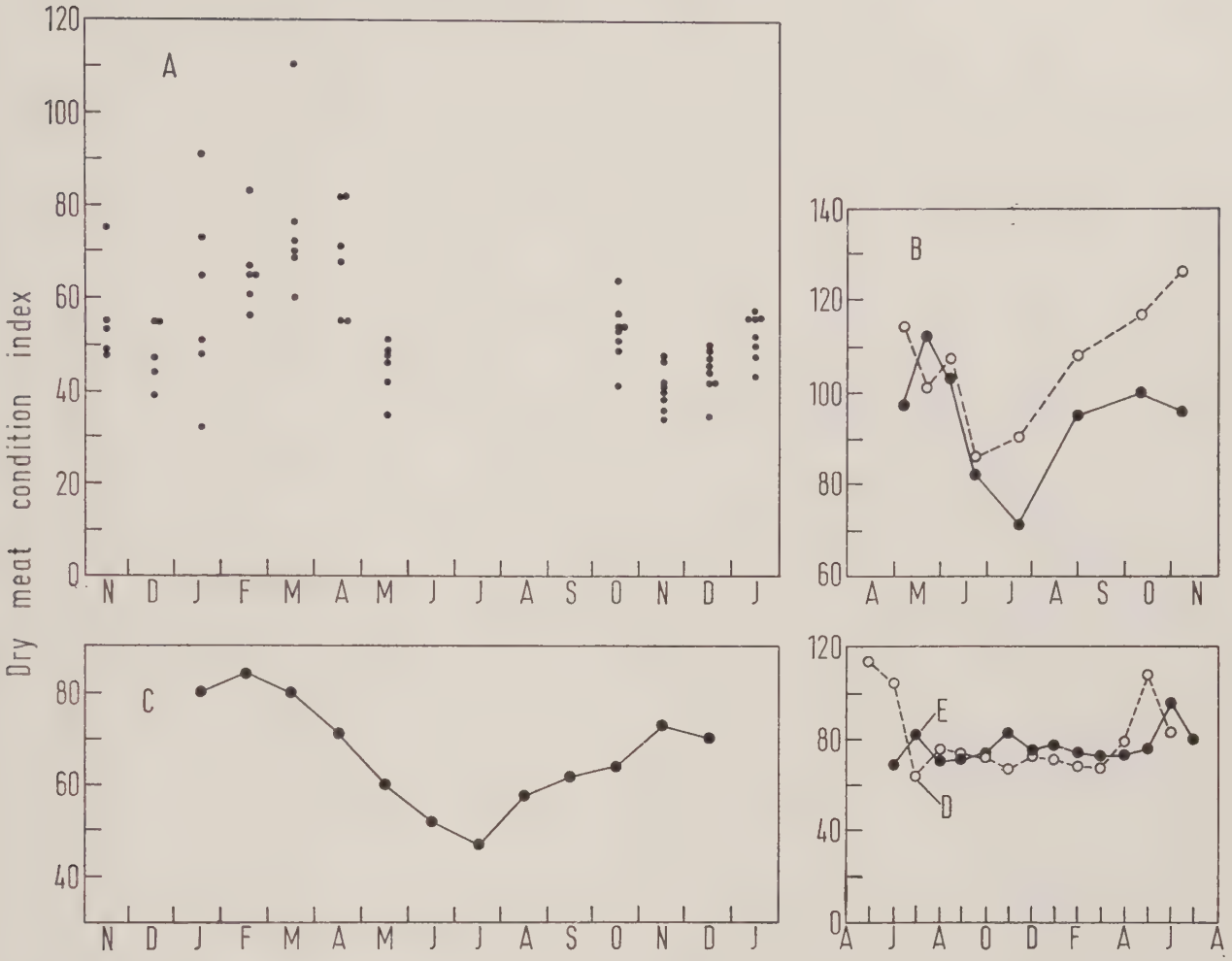


Figure 10 Seasonal variation of the dry meat condition index in *C. virginica*. The origins of the data are as follows: A Menzel and Hopkins (1952), B Medcof (1946). Solid circles and full line are samples from the upper part of the Bideford River, and open circles and broken line from the lower, C Sakuda (1966).
D Haven (1962) York River } composite curves of four years'
E Haven (1962) Rappahannock River } observations.

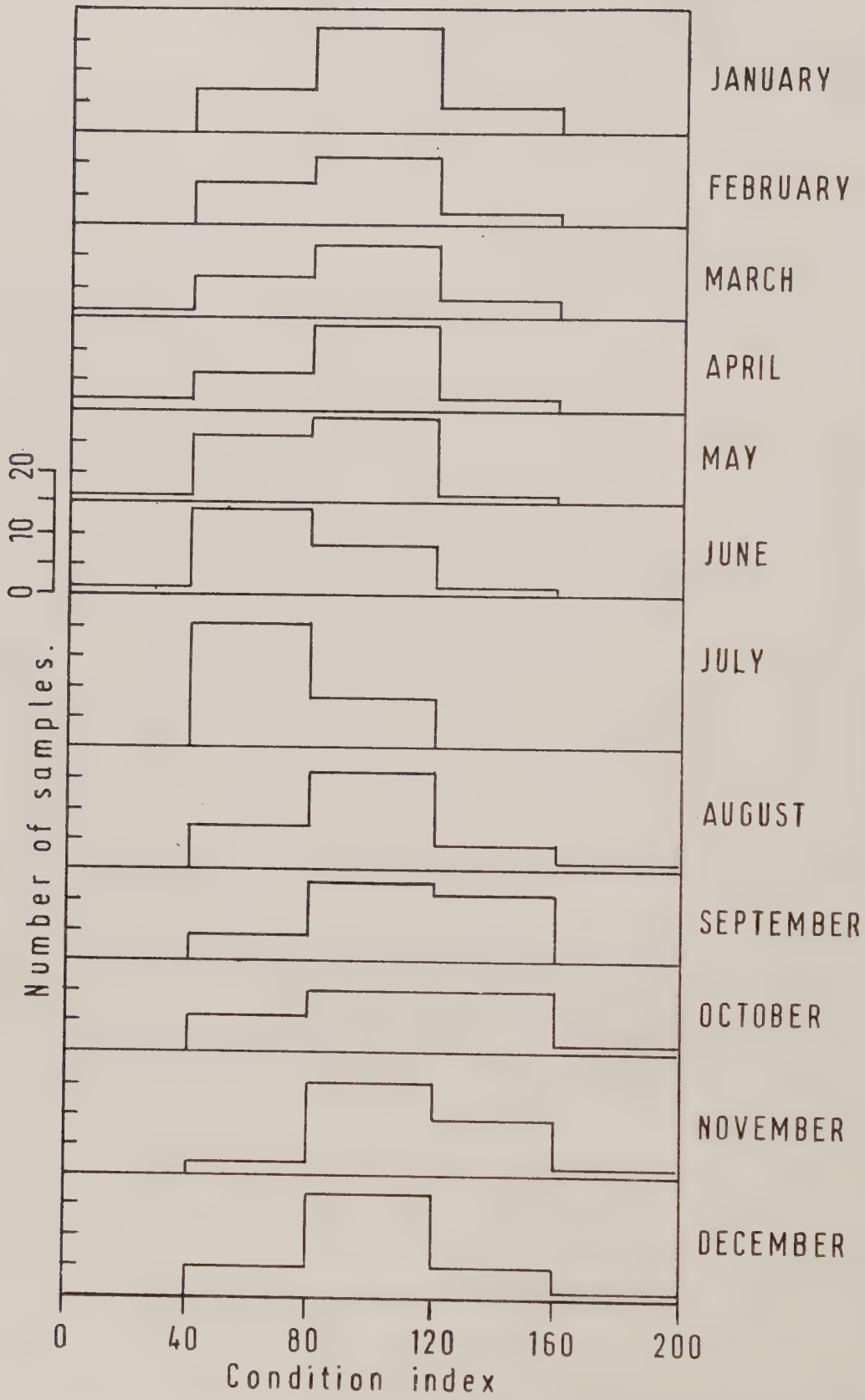


Figure 11 Seasonal variation of the dry meat condition index in *Ostrea lurida*. The histogram shows the number of samples in each of five categories. Calculated from Westley (1959–63).

DISCUSSION OF THE LITERATURE

All these published data have been examined and, where possible, the chemical analyses have (when necessary) been recalculated on a dry weight basis, to give condition indices according to the formula on page 3.

DRY MEAT CONDITION INDEX

With the exception of Milroy (1909) and Millar (1961) who estimated an index based on wet flesh, the published information deals with a dry meat condition index. It can be argued that from the commercial viewpoint it is the volume of meat that is important, but for biological purposes it is the protein, fat and carbohydrate content that is significant. There is some difficulty in obtaining consistent results between different observers in estimating the weight or volume of wet flesh, and recently Shaw *et al.* (1967) have drawn attention to the way in which changes in water content can disguise changes in the dry meat condition index. For these reasons, indices which are based on wet flesh are not discussed in this paper.

Data have been published for nine oyster populations and these are summarized as cumulative curves in Figure 8 (see also the results of the present work, in Figure 2A). Table 5 presents a synopsis of the dry meat condition index and the glycogen content data by showing the values which were exceeded by 75, 50 and 25 per cent of the samples from each population. High indices were found in five populations where a substantial proportion of samples had a condition index greater than 100: the two *O. edulis* populations (Figures 2A and 8I), *C. virginica* from Canada (Figure 8A) and *C. gigas* and *O. lurida* from the State of Washington (Figure 8E, J). The population of *C. virginica* in the Gulf of Mexico (Figure 8B) was in notably poor condition, half the samples having an index below 60–80. These results suggest that populations in cooler waters (Canada, England and Wales, Holland) tend to be in better condition than those from warmer waters. For example, *C. virginica* from Chesapeake Bay (Figure 8D) is in rather better condition than from Lousiana (Figure 8B). Support for this view is shown in Figure 9 where the median values for the dry meat condition index (given in Table 5) are related to the latitude of the area where the population occurs. All the information is from the northern hemisphere and it is remarkable that a systematic relation appears to exist, in spite of the fact that the data are drawn from five species of oysters living in a wide variety of habitats. It would be most valuable if systematic studies could be made of the same species from a wide range of latitudes.

Details of the seasonal variation in the dry meat condition index (see Figures 3A, 10 and 11) are available for six populations. Generally a decline in condition was found in the summer months, although this was not invariable (e.g. Figure 10E). The results reported in this paper show that oysters at Tal-y-foel and the River Yealm remained in good condition throughout the summer (Table 1).

Westley's data, because of the considerable quantity, can be studied in more detail. He examined both *C. gigas* and *O. lurida*. *C. gigas* is not native to North America and it spawns only in favourable areas in the State of Washington; the fishery is supported by regular supplies of spat from Japan. For this reason the growth pattern, particularly in relation to spawning, may be distorted, and therefore the seasonal variation has not been analysed. *O. lurida* is native to the area and Figure 11 shows the number of samples in each of five categories of condition for each month in the years 1956–1962. The distribution was constant until May, the 80–120 index range being the most numerous group; this fell in June and July, when the 40–80 range became the most numerous. Hopkins (1937) has shown that spawning commences in May and is at its maximum in June and July. Recovery was swift in August, and by September and October samples with an index over 120 were more numerous than at any other time of the year.

Shaw *et al.* (1967) point out that a high dry meat weight index is positively correlated with a low percentage of water. Although their curves correspond well, other results reported in the literature show that the relation is not necessarily very close. For example, Menzel and Hopkins (1952, Tables 42 and 96) published both the dry meat weight index and the percentage of water in the flesh, and these data show only a general relationship between the two parameters. Of course the determination of the water content

of the meat is liable to the same experimental hazards as estimating a condition index based on either the weight or volume of the wet flesh.

Engle (1958) estimated the percentage of solids in monthly samples of *C. virginica* collected in the upper part of Chesapeake Bay. His Figure 3, giving the average results for seven years, shows that the meats were thinnest in August, when they contained only 13–14 per cent solids; during the winter months the solids rose to 16–19 per cent. Galtsoff *et al.* (1947) working in two estuaries in the lower part of this bay obtained rather different results, the percentage of solids being higher in the summer and low in the winter. Haven (1962) examined oysters from the same area and his results show that in the York River the low level of the dry meat condition index of the summer months continued well into the winter (Figure 10D); in contrast, the population from the nearby Rappahannock River had only rather small fluctuations throughout the year (Figure 10E).

From these various results it appears that condition is often high in the winter months and declines to a lower level during the summer. At this period the animal is spawning, and the temperature is most suited to rapid growth. It is possible that part of the seasonal fluctuation in the condition index may be explained by meat growth failing to keep up with the growth of the shell. This could be caused by lack of food in the winter or by weight losses due to spawning, or by a combination of these factors.

Table 6 The correlations (all positive) between fat and carbohydrate (or glycogen) content of oysters when both are expressed as a percentage of the protein

Species	Author	Correlation of fat with glycogen or carbohydrate	Degrees of freedom	Level of significance of correlation (%)
Crassostrea virginica	Lee *et al.* 1960	Carbohydrate	11	1
Crassostrea gryphoides	Durve and Bal 1961	Glycogen	22	5
	Venkataraman and Chari 1951	Glycogen	23	1
Crassostrea gigas	Hatanaka 1940	Glycogen	7	*None*
	Masumoto *et al.* 1934	Carbohydrate	86	1
Crassostrea angulata	Graca *et al.* 1956	Carbohydrate	24	1
	Establier 1966	Carbohydrate	25	1
Crassostrea commercialis	Humphrey 1941	Glycogen	18	*None*
Ostrea edulis	Russell 1923	Carbohydrate	44	*None*
	Gaarder and Alvsaker 1941	Glycogen	16	*None*
	Krvaric 1953	Glycogen	10	10
Ostrea lutaria	Malcolm 1929	Glycogen	6	1

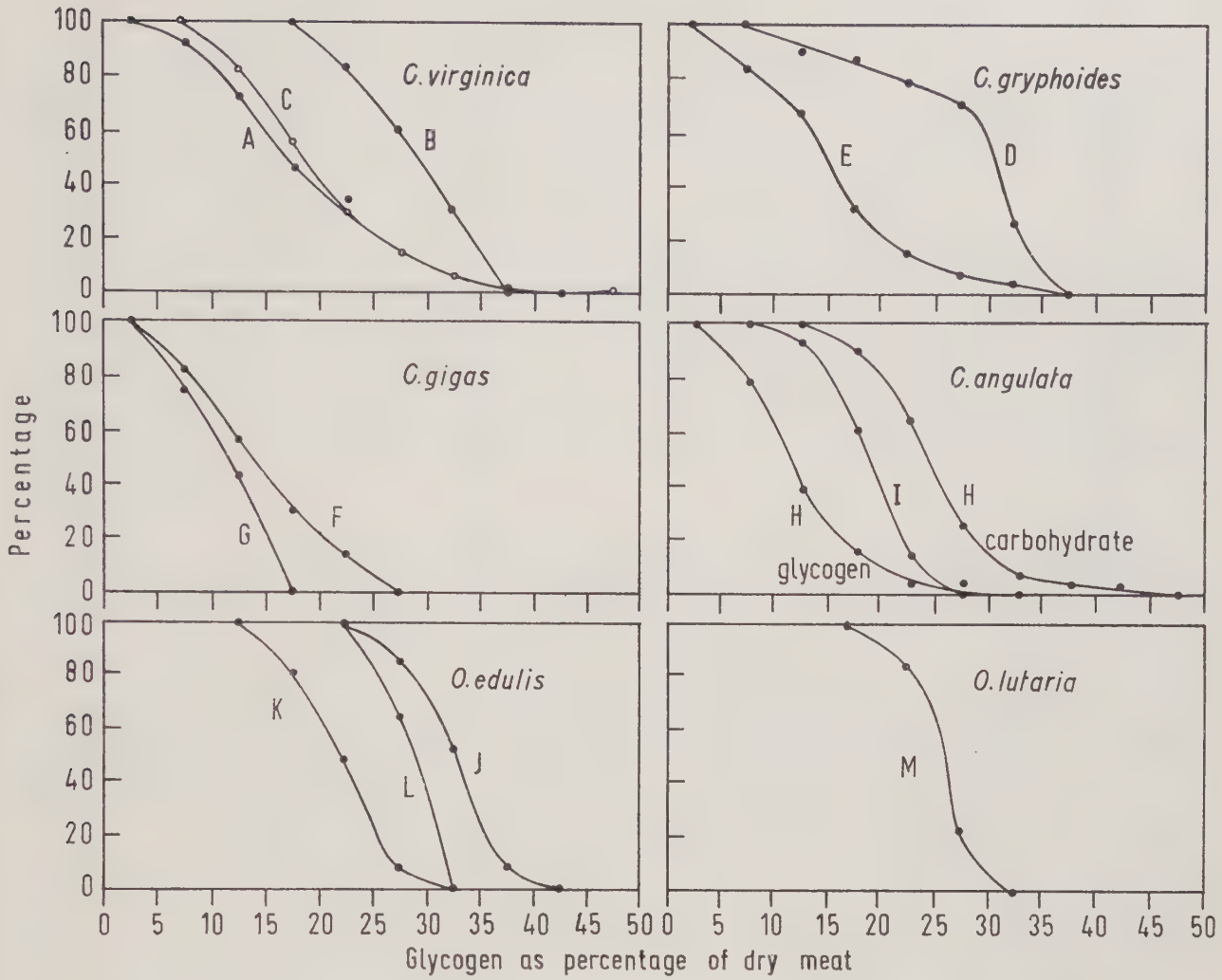


Figure 12 Cumulative curves showing the proportion (vertical scale) of samples which exceeded successive values of glycogen (or carbohydrate), expressed as a percentage of the dry meat weight. Curves B, F, I, J refer to percentage carbohydrate found by difference; all the rest refer to percentage glycogen found by direct analysis. The origin of the data and the species concerned are as follows: *C. virginica*—A Galtsoff *et al.* (1947), B Lee *et al.* (1960), C Menzel and Hopkins (1952); *C. gryphoides*—D Durve and Bal (1961), E Venkataraman and Chari (1951); *C. gigas*—F Masumoto *et al.* (1934), G Hatanaka (1940); *C. angulata*—H Graca *et al.* (1956), I Establier (1966); *O. edulis*—J Russell (1923), K Krvaric (1953), L Gaarder and Alvsaker (1941); *O. lutaria*—M Malcolm (1929).

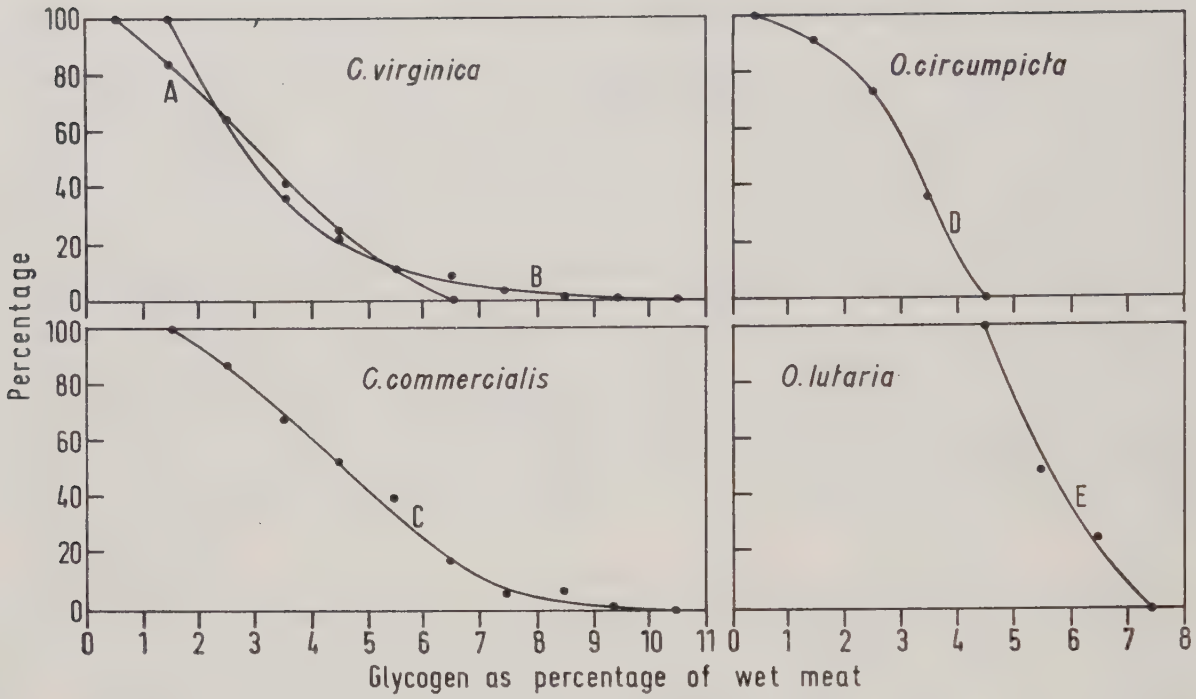


Figure 13 Cumulative curves showing the proportion (vertical scale) of samples which exceeded successive values of glycogen, expressed as a percentage of the wet weight. The origin of the data and the species concerned are as follows: *C. virginica*—A Galtsoff *et al.* (1947), B Menzel and Hopkins (1952); *C. commercialis*—C Humphrey (1941); *O. circumpicta*—D Okazaki and Kobayashi (1929); *O. lutaria*—E Malcolm (1929).

GLYCOGEN (OR CARBOHYDRATE) CONTENT

The glycogen content of oysters has attracted attention for a long time and there are a good number of analyses recorded in the literature. Generally the results are given as a percentage of the dry meat weight, and Figure 12 presents the cumulative curves of the results from thirteen populations of oysters (see also the results of the present work, in Figure 2C and Table 5). Figure 13 summarizes similar analyses on a wet meat basis in five populations.

On a dry meat basis the maximum glycogen content is usually about 30–35 per cent of the dry weight, but the median value varies a good deal (Table 5). For example, Galtsoff *et al.* (1947) found in Chesapeake Bay that half their samples had less than 18 per cent glycogen. This may be contrasted with the equivalent value of 34 per cent for *O. edulis* reported in this paper. The value of 29 per cent calculated from the data of Lee *et al.* (1960) seems to be high for *Crassostrea*; it may be due to the fact that the samples were collected from shucking houses and were therefore biased towards stock which was in good condition. Although the median value varies considerably the upper limits seem to be less systematically varied.

When large numbers of samples are examined from areas which normally have a low glycogen content, occasional samples are found with values as good as those from the best areas, e.g. Louisiana (Menzel and Hopkins 1952).

Details of the seasonal variation in glycogen content are given in a number of papers and these results are summarized in Figure 14. Where the inclusion of protein analyses make it possible, the glycogen (or carbohydrate) has been calculated as a percentage of the protein content. The approximate duration of the breeding season is also indicated. The figure shows clearly that the glycogen content—whether considered as a percentage of the flesh or related to a constant amount of protein—declines during the breeding season. Conspicuous examples are demonstrated for *Crassostrea* in Figure 14A, B, C, D and F. The loss of genital products—the embryos of *Ostrea edulis* contain 13–15 per cent glycogen (Collyer 1957)—is also accompanied by a loss of protein, but the data show that the protein: glycogen ratio changes, and it is the cause of this change of ratio that is of interest.

It is possible that much of the glycogen is used as an additional energy source during the period of rapid proliferation of the gametes, supplementing that being obtained from the food. Matsumoto *et al.* (1934), who give a very long series of analyses, hint that some of the glycogen is converted to fat, based on the fact that the maximum weight of glycogen per animal is reached a little earlier (April) than the maximum weight of fat (May); this point has been amplified in reviews by Giese (1966) and Goddard and Martin (1966). This may be so for a short period, but for most of the year the curves of fat and glycogen content are very close; when the glycogen content rises or falls the fat content changes in a similar manner.

Most authors have considered glycogen to be the major energy reserve in oysters, but the role of fat also requires consideration. Giese (1966) suggests that if a tissue contains more than 2–5 per cent of lipid then some is present as a reserve, as opposed to structural lipid. The literature frequently reports oysters containing 10–15 per cent of fat and it appeared relevant to examine the published data for evidence of a relation between fat and glycogen accumulation. Millar and Scott (1967) record that the dry organic matter of *O. edulis* larvae contains considerably more lipid than carbohydrate.

A search of the literature revealed twelve papers (listed in Table 6) in which the authors reported sufficiently detailed and numerous analyses for the calculation of regressions relating the glycogen (or carbohydrate) content to extractable fat. Where a significant correlation was found, the data are plotted in Figure 15. In seven sets of data there was a significant positive correlation (six significant at the 1 per cent level and one at the 5 per cent) between the amount of fat and amount of glycogen. One of the remaining five sets was positively correlated at the 10 per cent level (Krvaric 1953); in the remaining four sets there was no correlation. It is important to note that in none of the twelve sets of data was a negative correlation found. Humphrey (1941) examined 40 individual oysters and found a positive correlation (significant at the 1 per cent level) between fat and glycogen when both were expressed as percentages of the nitrogen content, but in an examination of 20 samples from the Georges River in August 1940, no correlation was found.

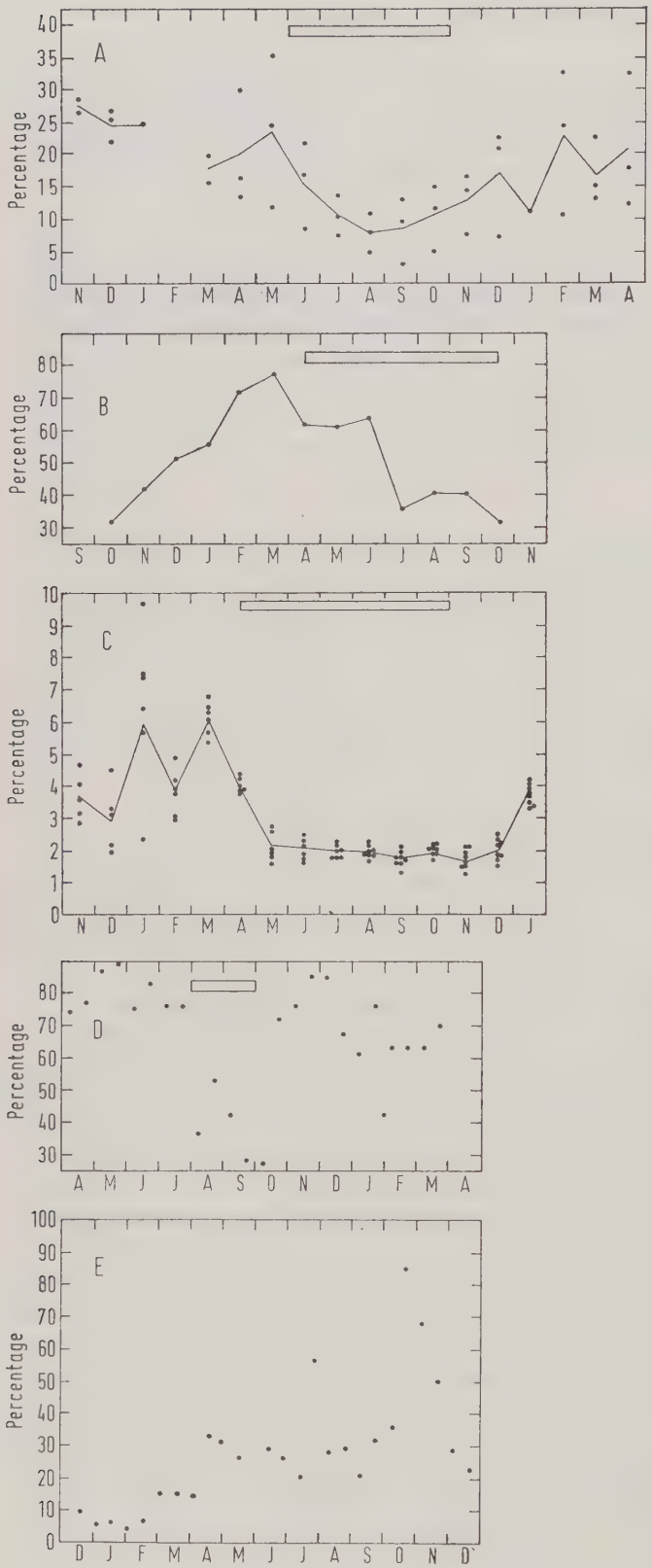
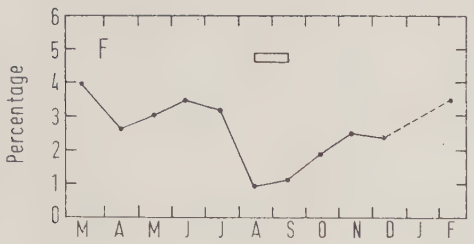


Figure 14 The seasonal variation in the proportion of glycogen (or carbohydrate) in the tissues of oysters. Figures B, G, H, I and J refer to carbohydrate; all the others to glycogen. The bases are as follows:
C, F, K as a percentage of the wet meat;
A as a percentage of the dry meat;
B, D, E, G, H, I, J, L, M, N, O as a percentage of protein.
The shaded horizontal bars show, where known, the approximate duration of the spawning season. The origin of the data and the species concerned are as follows:

C. virginica
A Galtsoff *et al.* (1947)
B Lee *et al.* (1960)
C Menzel and Hopkins (1952)
C. gryphoides
D Durve and Bal (1961)
E Venkataraman and Chari (1951)
C. circumpicta
F Okazaki and Kobayashi (1929)
C. gigas
G Masumoto *et al.* (1934) ♀ animals
H Masumoto *et al.* (1934) ♂ animals
C. angulata
I Graca *et al.* (1956)
J Establier (1966)
C. commercialis
K Humphrey (1941)
O. edulis
L Russell (1923)
M Gaarder and Alvasaker (1941)
N Krvaric (1953)
O. lutaria
O Malcolm (1929).


F
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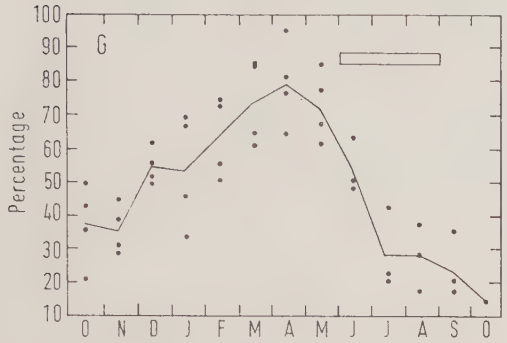
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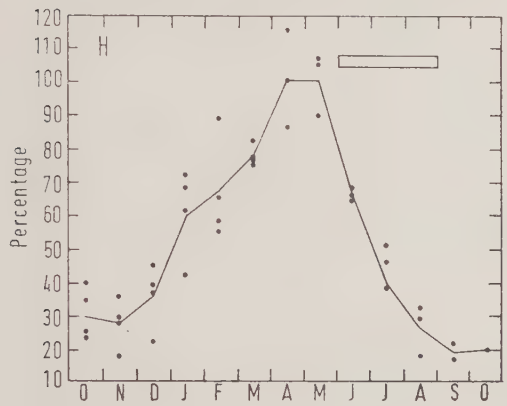
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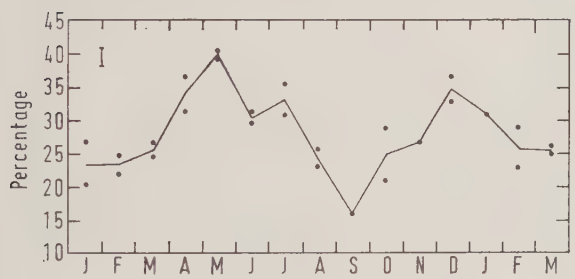
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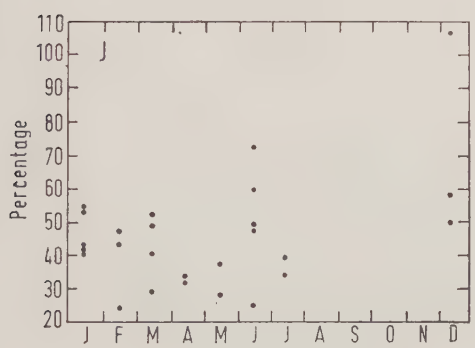
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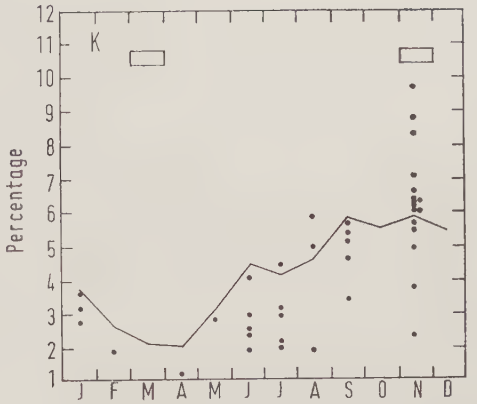
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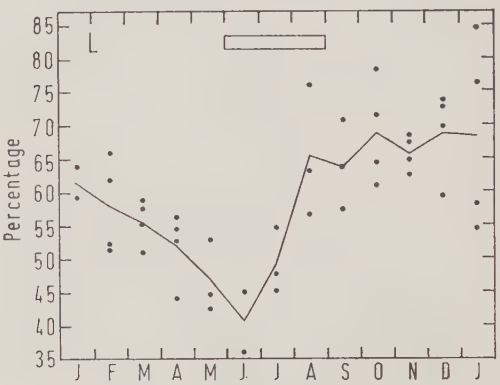
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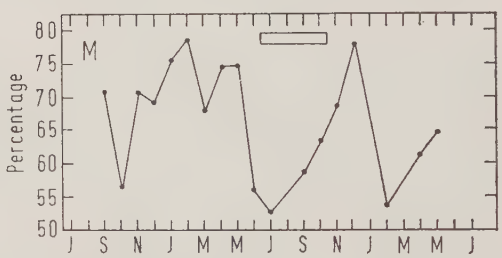
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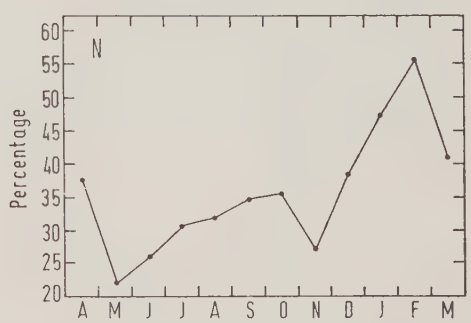
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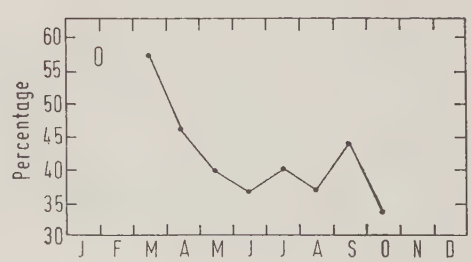
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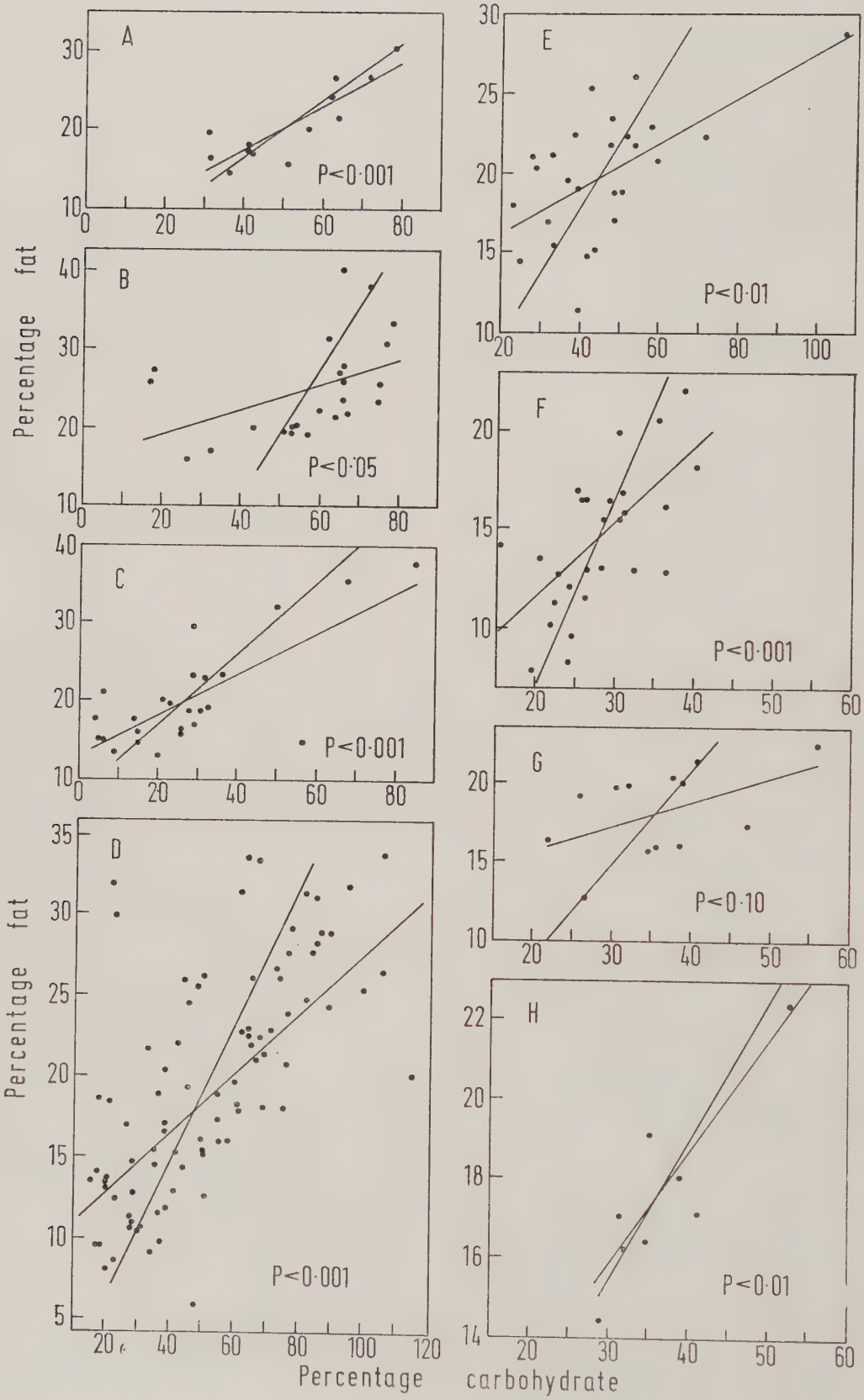
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B
P<0·05
C
P<0·001
D
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E
P<0·01
F
P<0·001
G
P<0·10
H
P<0·01
Percentage fat
Percentage fat
Percentage carbohydrate

From these correlations the average weight of fat corresponding to various levels of carbohydrate can be calculated. When the weight of carbohydrate per animal is 50 per cent of the protein weight—about the middle of the range—the weight of extractable fat is, on average, 21.7 per cent of the protein weight, with a range, in different populations of oysters, of 19 to 26 per cent. Conversely, when the fat content is 20 per cent of the protein weight, the average carbohydrate content is 43.4 per cent, with a range from 27 to 51 per cent. These figures imply that in an oyster containing a unit amount of protein the weight of fat will be approximately half that of the weight of carbohydrate. Since the calorific value of fat is about twice that of the same weight of carbohydrate, the calorific value of the two reserves is approximately equal.

This evidence strongly suggests that, in some populations, when conditions are good, fat and glycogen are accumulated, and when conditions are bad both reserves are lost to a similar degree. Those populations which did not reveal any correlation between the two reserves may have been behaving in a different manner, or the results may have been affected by the experimental techniques employed. It is remarkable that no inverse relation between fat and glycogen (or carbohydrate) has been found. Yonge (1926) examined the digestive enzymes of *O. edulis* and stressed the emphasis on the digestion of carbohydrates. Two recent studies (Haven 1965, Gillespie *et al.* 1966) have demonstrated an increase in dry meat in *C. virginica* fed with corn-starch or wheat flour as a supplement to sea water. Unfortunately, although Gillespie *et al.* measured the glycogen content of their animals, in neither study was fat measured. Mitchell (1917) claimed to have obtained a substantial increase in percentage fat in only 48 hours in oysters kept in 0.25 per cent glucose or dextrose, but this experiment has not been repeated.

The next point for inquiry is the uses to which these reserve materials are put by the oyster. The fall in glycogen at the time of spawning has led to the suggestion that this reserve is particularly used in the preparation of gonad material, but the results quoted in this paper show that glycogen does not fall in greater proportion than fat. Indeed the glycogen content of *Ostrea edulis* which have spawned within a few days of analysis is not particularly low (Table 3). Similarly, the glycogen content of recently liberated larvae is probably no higher than the stock from which they came (Collyer 1957). Fat would appear to be the more important reserve at that stage (Millar and Scott 1967).

It was pointed out by von Brand (1945) that glycogen is the most common energy source in anaerobic respiration. The rate of loss of glycogen during the winter months seems to be too slow for this to be important during the period when adverse conditions might be expected. Baker *et al.* (1942) stored oysters in the air at 4°C, and although the glycogen content did decrease, it was many weeks before the effect appeared. Humphrey (1941) found no consistent decline over a period of 42 days. Conversely, it seems unlikely that conditions in the summer months would require substantial periods of anaerobic respiration.

Summer is a period of higher temperatures and hence higher activities. If the food supply was inadequate this could be at least a partial explanation for the loss of food reserves. Collier (1959) has shown how the pumping activity of an oyster could use up all of its glycogen reserve in about 400 hours (less than 17 days) if there was no replenishment. Although the same paper suggests a mechanism by which pumping activity and food intake are brought into line by the oyster, the regulation is not necessarily complete, and activity and growth of shell could outstrip the food supply.

Figure 15 The relation between fat (vertical scale) and glycogen (or carbohydrate) content of oysters, expressed as a percentage of the total protein. Figures A, D, E and F refer to carbohydrates; all the rest to glycogen. The two calculated regression lines are shown and the level of significance is indicated on each figure. The origin of the data and the species concerned are as follows: *C. virginica*—A Lee *et al.* (1960); *C. gryphoides*—B Durve and Bal (1961), C Venkataraman and Chari (1951); *C. gigas*—D Masumoto *et al.* (1934); *C. angulata*—E Graca *et al.* (1956), F Establier (1966); *O.edulis*—G Krvaric (1953); *O. lutaria*—H Malcolm (1929).

ACKNOWLEDGEMENTS

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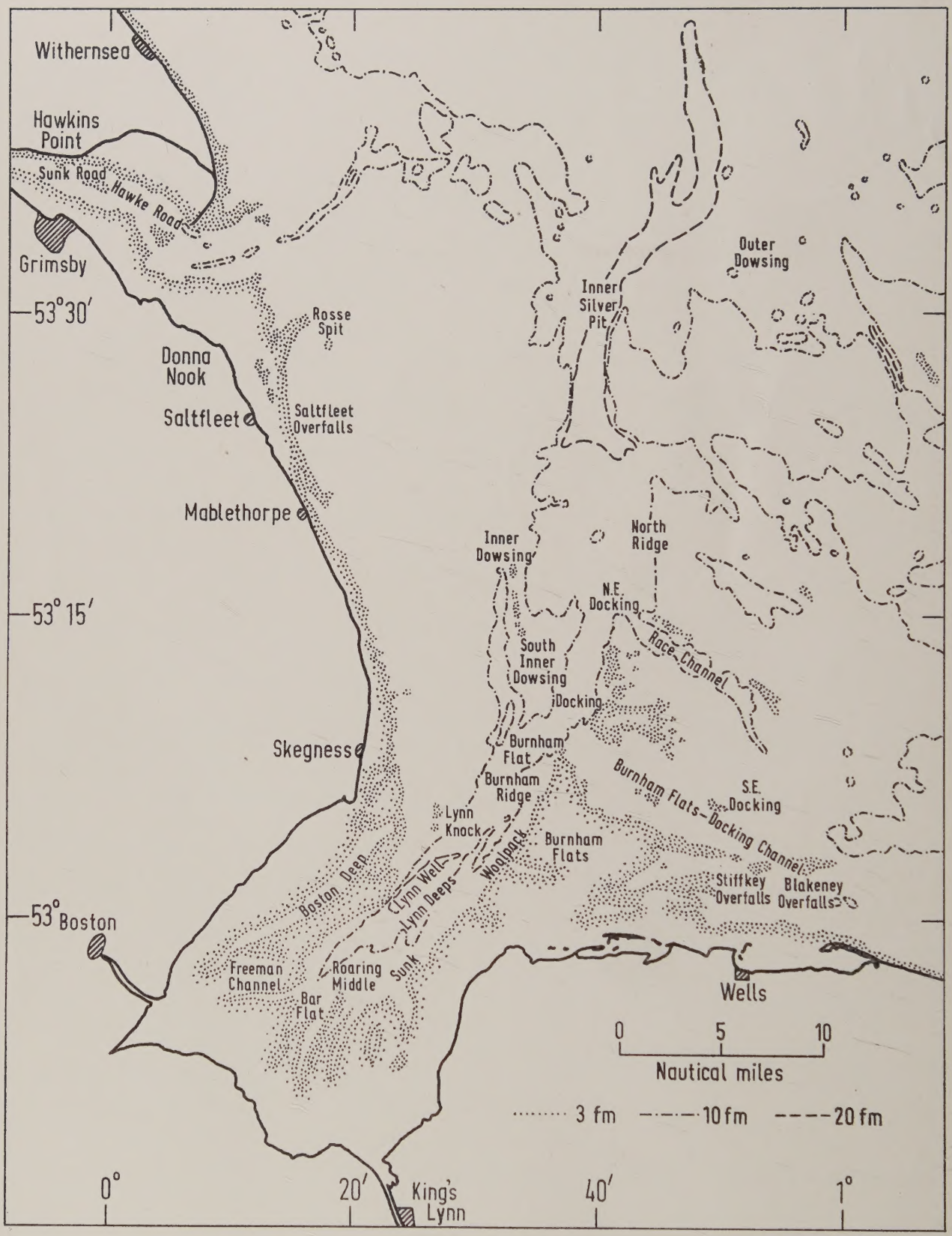

Frontispiece General topographical chart of the Wash area.